ECOLOGICAL AND GENETIC STUDIES ON HEADING TIME AND ITS CONSTITUENT TRAITS IN WHEAT(Dissertation_全文)

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CHAPTER I. INTRODUCTION

In Southwest Japan, wheat is generally sown in the autumn and harvested in the early summer. The adaptation to a certain temperature condition is required at each growth stage to achieve a high and stable grain yield. Freezing injury of shoot apex in the winter (GOTOH 1975; GEORGE 1982), sterility caused by low temperature at heading stage (MARCELLOS and SINGLE 1984; KIM et al. 1985; QIAN et al. 1986), and reduction in grain size caused by high temperature during grain filling period (ASANA and WILLIAMS 1965; SOFIELD et al. 1977) must be especially avoided. As to freezing injury, shoot apex must be retained below the soil surface by preventing both the initiation of spikelet primordium and stem elongation (GOTOH 1975; GEORGE 1982). These two damages can be avoided by controlling heading time in the field (simply called "heading time", hereafter) so as to flower at an optimum time in each locality. These facts clearly indicate that heading time is an important character for wheat breeding.

Breeding strategy of heading time is complicated because heading time of wheat is a complex character determined by several heading traits. The first trait refers to the requirement of low temperature necessary for the commencement of reproductive growth. This trait is hereafter called "chilling requirement", though it has been given various terms, such as "growth habit" (WADA and AKIHAMA 1934; KAKIZAKI and SUZUKI 1937; YASUDA and SHIMOYAMA 1965), "vernalization response" (HALLORAN and BOYDELL 1967; SYME 1968; HALSE and WEIR 1970; PUGSLEY 1971; RAHMAN 1980; HOOGENDOORN 1984; ROBERTS 1986), and "vernalization requirement" (SNAPE et al. 1976; GOTOH 1976; RAO and WITCOMBE 1977). The second trait refers to the retardation or acceleration of heading in response to day-length condition, and is called "photoperiodic response" (TAKAHASHI and YASUDA 1958). The third trait refers to the earliness of fully vernalized plants under optimum condition for reproductive growth. This trait is hereafter called "narrow-sense earliness" after TAKAHASHI and YASUDA (1958), though this also has been called in different terms, such as "earliness per se" (HUNT 1979; HOOGENDOORN 1985a), "basic development rate" (FLOOD and HALLORAN 1984a), and "intrinsic earliness" (MASLE et al. 1989). The fourth trait refers to the retardation or acceleration of heading in response to temperature conditions subjected after full vernalization as indicated by GOTOH (1977) and FLOOD and HALLORAN (1984a), and is called "thermal response" (GOTOH 1977). According to YASUDA and SHIMOYAMA (1965), though there was no varietal difference in this trait, the first three traits were all closely related with heading time in Kurashiki, Japan. Among the three traits, photoperiodic response proved to be the most important trait in the control of heading time, followed by growth habit and narrow-sense earliness. Accordingly, these three traits other than thermal response were studied in this study as the constituent traits of heading time.

Approaching from another stand point, EVANS et al. (1975) pointed out that the influence on wheat adaptation might be different among the traits: Chilling requirement is important for the adaptation to winter coldness and photoperiodic response is necessary for avoiding the damage caused by late frost. It was thus indicated that the adaptability of wheat varieties should be improved more efficiently by taking into account not only these three traits themselves but also their combination in order to adopt a breeding strategy of heading time. The advantage of such a breeding strategy was also pointed out by HASHIMOTO and HIRANO (1963), HUNT (1979), and YOSHIDA et al. (1983). However, little is known about the influence of narrow-sense earliness on wheat adaptation, and EVANS et al. (1975) provided no data from which the influence of the other two traits could be deduced as mentioned above. Such being the case, it is still impossible to predict the best combination of the three traits for the breeding of heading time in each locality.

The following ecological studies seem to offer a clue to the influence of each trait on the adaptation to growing environments.

a) Heading time in diverse areas or under diverse growing environments is examined using a relatively small number of varieties which represent the major genetic variation in each trait. The influence of each trait should be deduced by analyzing the relationship between the three heading traits, heading time and the growing environments at each experimental site.

b) Heading time is examined at a certain place by using a great number of wheat varieties collected from diverse areas. As each variety is adaptive to its respective area, the influence of each trait can be deduced by analyzing the relationship between the three heading traits, heading time and the growing environments of the area of collection. Of these, the first strategy is practically difficult because an international collaborative work is required to prepare a wide variation in growing environments. Accordingly, the second strategy is recommended as the first step, though the conclusion reached is not necessarily valid for the areas with different growing environments. However, there has so far been no report of analysis carried out from such a stand point, though several studies have shown that varietal difference in the responses to vernalization and photoperiod could be well explained by the difference in growing environments of cultivated areas (WADA and AKIHAMA 1934; SYME 1968; WALL and CARTWRIGHT 1974; HUNT 1979; FORD et al. 1981; HOOGENDOORN 1985b).

Among the three traits, only narrow-sense earliness can be evaluated independently of the other two traits, as it is measured by the growth period of fully vernalized plants under long-day condition (TAKAHASHI and YASUDA 1958). Photoperiodic response can be evaluated independently of chilling requirement, as it is usually measured by the difference in the growth period of fully vernalized plant between short-day and long-day conditions (TAKAHASHI and YASUDA 1958). However, it is still a matter of argument if photoperiodic response such measured is independent of narrow-sense earliness (SNAPE personal communication). The most complicated trait is chilling requirement because it is difficult to know whether a wheat plant is fully vernalized or not. As no investigation has so far been succeeded in evaluating chilling requirement independently, it has been indirectly estimated by growth habit (KAKIZAKI and SUZUKI 1937; YASUDA and SHIMOYAMA 1965), vernalization response (SYME 1968) and vernalization requirement (GOTOH 1976). Although GOTOH (1976) especially attempted to evaluate chilling requirement itself, vernalization requirement proved to partly include the effect of narrow-sense earliness. Therefore, prior to the analysis of the influence of these heading traits on wheat adaptation, the evaluation method of these traits must be first established.

Genetic aspects of the adaptation strategy must be also studied to find out the availability of each gene, which is responsible for respective heading traits, for wheat breeding. As for chilling requirement which is examined in this thesis, the genetic basis has been studied by many researchers (SEARS 1954; KUSPIRA and UNRAU 1957; MORRISON 1960; TSUNEWAKI and JENKINS 1961; TSUNEWAKI 1966; LAW 1966; HALLORAN and BOYDELL 1967; PUGSLEY 1971,1972). As reviewed by FLOOD and HALLORAN (1986), it was clearly shown that five genes, Vrn1, Vrn2, Vrn3, Vrn4 and Vrn5, were responsible for reducing chilling requirement, and that the carrier of at least one of them was spring wheat. Although gene action of Vrn5 is not clear, according to GOTOH (1976), Vrn1 is the most effective and gives complete insensitivity to vernalization. On the contrary, the three other genes, namely, Vrn2, Vrn3 and Vrn4 give partial insensitivity, with Vrn2 being weaker than the other two genes. These facts indicate that the adaptability should be different between Vrn genes, and that the gene most suitable to each locality should be utilized for wheat breeding. Therefore, the adaptability of Vrn genes must be evaluated by analyzing their geographical distribution.

From the point of view mentioned above, ecological and genetic studies on heading characters and the prerequisite methodological studies were carried out. The subjects discussed in the present study are summarized as follows. Evaluation method of chilling requirement and narrow-sense earliness is successfully established in CHAPTER II. Using 158 wheat landraces of diverse geographical origins, evaluation method of photoperiodic response is also established, and then the influence of the three heading traits on wheat adaptation was deduced in CHAPTER III. The strategy of adaptation to diverse growing environments through the adjustment of heading time is discussed in CHAPTER IV. Genetic aspects of the adaptation to diverse growing environments through the adjustment of chilling requirement is discussed on the basis of geographical distribution of *Vrn* genes in CHAPTER V.

CHAPTER II. METHOD FOR EVALUATION OF CHILLING REQUIREMENT AND NARROW-SENSE EARLINESS OF WHEAT VARIETIES

Introduction

Early heading wheat varieties can not easily become adopted to the areas with late frost, while late heading ones which are harvested in the rainy season in the wet monsoonal zone often experience wet-injury which impairs both grain yield and quality. Thus heading time is one of the most important characters controlling the adaptability of wheat varieties, and no breeding program is valid unless enough attention is paid to this character.

However, breeding for heading time and for the characters linked with this character is difficult because heading time of wheat is a complex character, which is determined by the three traits, i.e. photoperiodic response, narrow-sense earliness and growth habit (YASUDA and SHIMOYAMA 1965). Therefore, it is essential for effective breeding that the above traits are exactly evaluated in breeding materials especially in the plants that will be used as cross parents, as shown by HASHIMOTO and HIRANO (1963), HUNT (1979), and YOSHIDA et al.(1983).

Of these three traits, photoperiodic response refers to the retardation or acceleration of ear emergence in response to day-length. It can be easily evaluated by the difference in the number of days from the fully vernalized stage to ear emergence between short-day and long-day conditions (TAKAHASHI and YASUDA 1958). Narrow-sense earliness, which refers to the earliness of fully vernalized plants under optimum condition for reproductive growth, can be expressed by the number of days from the fully vernalized stage to ear emergence under as high a temperature as to ensure optimum reproductive growth and a 24h day-length regime (TAKAHASHI and YASUDA 1958).

The third trait, i.e. growth habit, originally refers to the low temperature requirement necessary for the differentiation of reproductive organs. According to TAKAHASHI and YASUDA (1958), this trait can be evaluated without chilling treatment, i.e. only by the duration from sowing to flag leaf unfolding under a high temperature and 24h day-length regime. However, growth habit evaluated by this method includes not only the low temperature requirement but also the effect of narrow-sense earliness. In view of this fact, GOTOH (1976) suggested that growth habit should be represented by the "vernalization requirement", i.e. by the minimum duration of exposure to the low temperature required for full vernalization, and he developed a method to evaluate the minimum duration. This concept is relevant because vernalization requirement is independent of photoperiodic response and narrow-sense earliness. In his method, however, the minimum duration refers to the duration of chilling treatment which shortens the period from the end of the treatment to the unfolding of the flag leaf up to 34 days irrespective of the kind of variety examined. Therefore, the minimum duration estimated by this method is inevitably associated with some distortion resulting from narrow-sense earliness of the variety tested.

Therefore, a method for the accurate evaluation of the low temperature requirement necessary for full vernalization was developed and evaluated in a series of experiments involving various chilling treatments in 15 wheat varieties. In the present study, the minimum duration of the low temperature required for full vernalization is referred to as "chilling requirement" to distinguish it from the "vernalization requirement" proposed by GOTOH (1976), which includes the effect of narrow-sense earliness.

Basic concept for the evaluation of chilling requirement

As stated before, GOTOH (1976) attempted to evaluate the chilling requirement of wheat by the minimum duration of the chilling treatment (referred to as only "treatment" hereafter) necessary for full vernalization. However, he failed to evaluate accurately the minimum duration, i.e. chilling requirement. This is because the number of days from the end of the treatment to flag leaf unfolding (Dtf) was adopted as the index for determining the minimum duration of the treatment, as Dtf continuously decreases with the treatment duration and does not reach a plateau, as shown in Fig. 2a. He assumed that the plant whose Dtf does not exceed a certain level has already been fully vernalized, and, based on some experimental results, he fixed the duration of the treatment which reduces Dtf to 34 days as the criterion for estimating chilling requirement. However, wheat plant grows also during the treatment. Therefore, in this criterion, which was selected irrespective of the duration of the treatment, the varietal difference in narrow-sense earliness is not considered. For instance, even if chilling requirement of two varieties is identical, in a variety with a larger narrow-sense earliness the estimation of chilling requirement will be higher than in the other.

Therefore, for the accurate evaluation of chilling requirement the growth during the treatment as well as the growth after the treatment should be considered, and an index independent of narrow-sense earliness should be adopted. Therefore, we attempted to evaluate the growth increment during the treatment, on the basis of the following two assumptions:

(1) The growth increment at the 1st leaf unfolding stage is constant irrespective of the treatment duration.

(2) The growth increment up to the end of the treatment is proportional to the treatment duration as shown in Fig. 1.

Based on these assumptions, the number of days from the end of the treatment to the 1st leaf unfolding (Dt1) decreases in proportion to the treatment duration (X days). This relationship is formulated as follows:

$$Dt1 = -BX + a \quad (a>0,\ B>0) \qquad ---(1)$$

In this equation, "a" represents the Dt1 when X=0, namely, the number of days from forced sprouting (start of the treatment) to the 1st leaf unfolding (Do1) without chilling treatment, and "B" represents the relative growth rate during the treatment, namely, the ratio of the growth rate during the treatment to the growth rate after the treatment(=1). Therefore, the growth increment during X days under the treatment corresponds to the growth

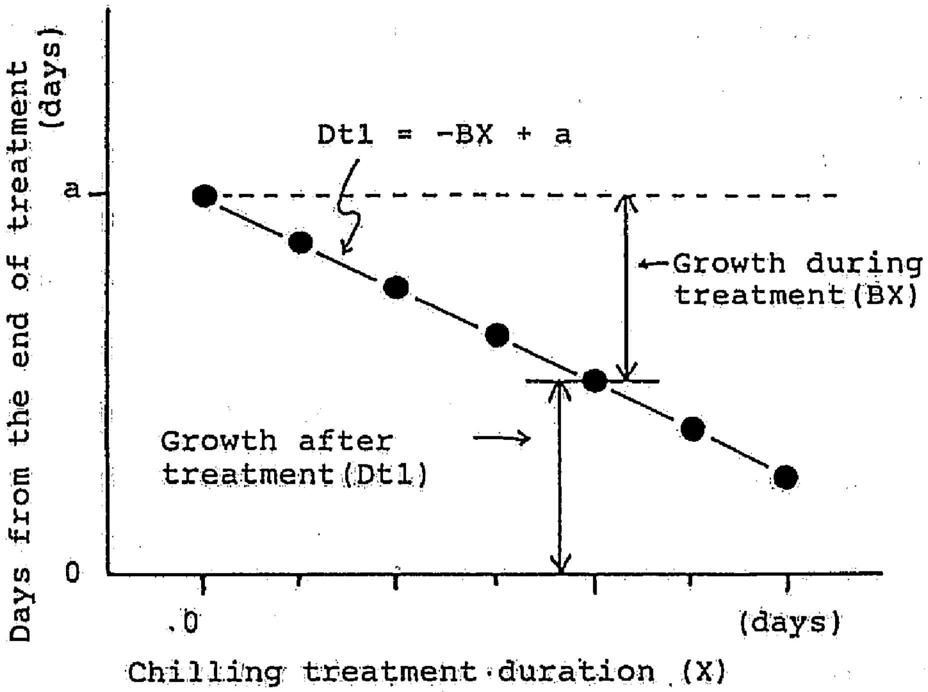

Fig. 1. Postulated decrease of Dt1 with the increase of chilling treatment duration. ●; Dt1 (Days from the end of chilling treatment to the 1st leaf unfolding)

increment during BX days after the treatment.

As seen from Equation (1), Dt1 changes depending upon the duration of the treatment, but this change is compensated by the corresponding change of BX, and thus the value (=a) of Do1 remains constant irrespective of the treatment duration. This means that the heading acceleration effects of various treatment durations can be compared by determining the number of days from the 1st leaf unfolding to flag leaf unfolding (D1f) or the days from forced sprouting to flag leaf unfolding (Dof). Both indices, D1f and Dof, are formulated as follows:

$$D1f = Dtf - Dt1 = Dtf + BX - a \qquad \text{---(2)}$$

$$Dof = Do1 + D1f = Dtf + BX \qquad \text{---(3)}$$

Here, attention should be paid to the fact that both D1f and Dof can be represented by the equation which involves BX, i.e. the growth increment during the treatment.

In a prolonged treatment exceeding the minimum duration necessary for full vernalization, no further acceleration of ear emergence occurs, and hence, as shown in Fig. 2, both D1f and Dof exhibit the same respective values as those observed in the treatment with the minimum duration necessary for full vernalization. Thus, the minimum duration of the treatment for full vernalization can clearly be determined by the duration of the treatment which reduces D1f or Dof to the constant value.

The values of Do1, D1f and consequently Dof are all intrinsic to a variety, although the latter two depend on the degree of vernalization of the plants and the conditions under which the plants grow. Based on the concept of narrow-sense earliness (TAKAHASHI and YASUDA 1958), the Dof of the plants which were

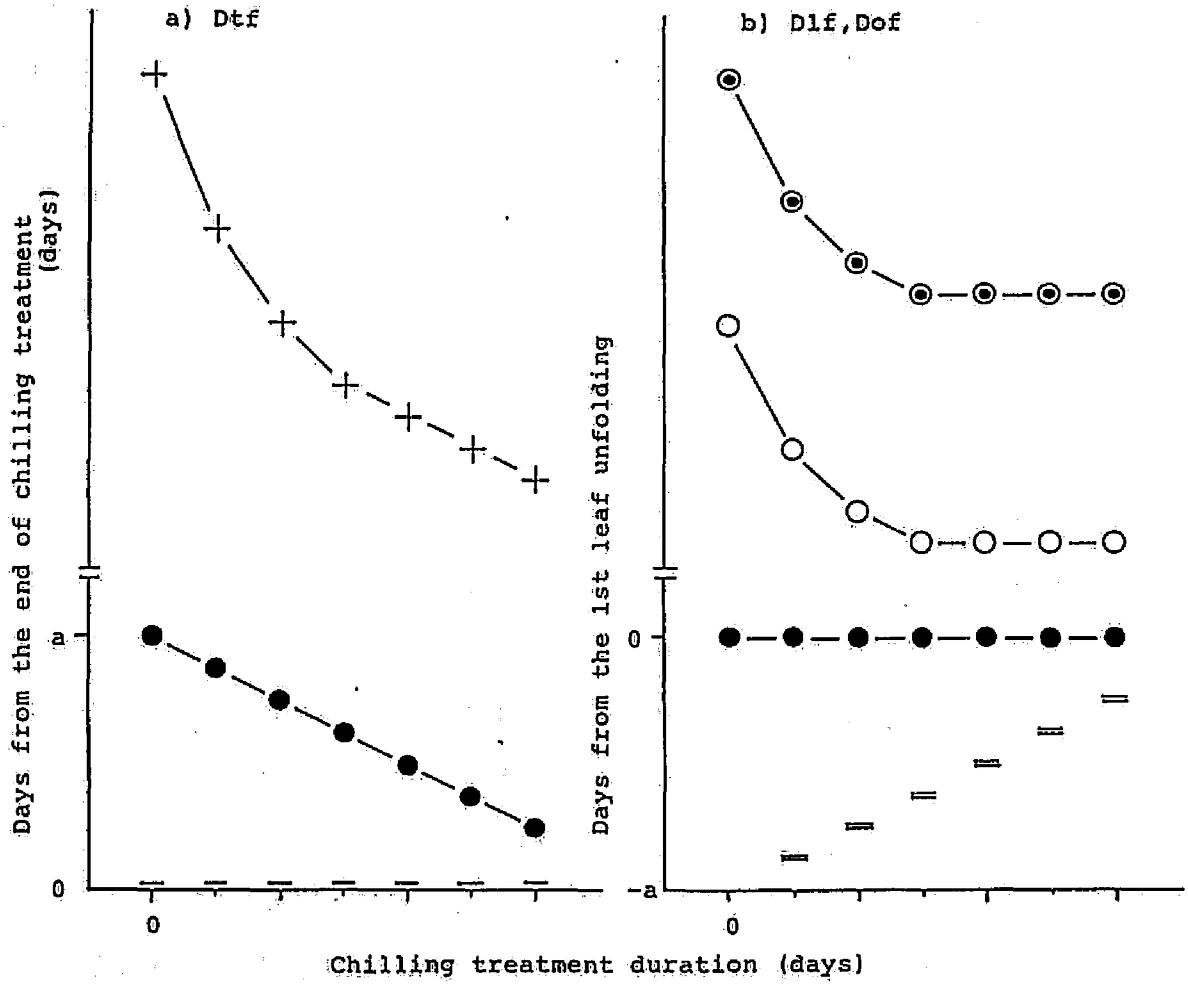

Fig. 2. Plant-development model: Postulated change of Dtf, Dlf and Dof with the increase of chilling treatment duration.
● ; Unfolding time of the 1st leaf, +; Dtf, O ; Dlf, ⊙ ; Dof, = ; End of chilling treatment

fully vernalized and grown under both high temperature and 24h day-length, represents also narrow-sense earliness of the varieties to which the plants belong.

Thus Dof may be the most suitable index for evaluating both chilling requirement and narrow-sense earliness of a wheat variety.

The notations for the number of days to leaf unfolding used in this study are presented in Table 1.

Materials and Methods

Using a total of 15 wheat varieties (*Triticum aestivum* L.) covering a wide range of growth habit(KAKIZAKI and SUZUKI 1937), seven experiments involving various durations of chilling treatment were successively conducted, as shown in Table 2. In each experiment, seeds of the materials were soaked in water for 24 hours at 20°C so as to enable them to sprout uniformly. They were sown in small soil-filled containers at a spacing of 2cm (between hills) x 3.5cm(between rows), then subjected to chilling treatments(5°C) for various durations under a 24h day-length regime. The time of seed soaking was adjusted to the treatment duration so that all the treatments would be completed simultaneously. Soon after the end of the treatment, the containers were transferred into a phytotron under a 20°C and 24h day-length regime. Then the number of days to flag leaf unfolding (Dtf) was scored to estimate Dof (=Dol+Dlf=Dol+Dtf-Dtl). Finally, the response of Dof to the treatment duration was examined to determine the suitability of Dof as the index for

Table 1. Notation for the days to leaf unfolding used in this study

Abbr.	Days to leaf unfolding
Dol	Days from forced sprouting to the 1st leaf unfolding*
Dof	Days from forced sprouting to flag leaf unfolding*
Dlf	Days from the 1st leaf unfolding to flag leaf unfolding*
Dtl	Days from the end of chilling treatment to the 1st leaf unfolding
Dtf	Days from the end of chilling treatment to flag leaf unfolding

*; The number of days under chilling treatment was adjusted to the number of days expected under post-treatment conditions as described in the text.

Table 2. Outline of 7 experiments in this chapter

Exp. No.	Date of exp.[1)]	Variety used		Heading[2)] time	Whole range of[3)] treatment durations
		Abbr.	Name		
1	1981. 3.26.	ASS	Akasabishirazu 1	41.5	0-85(days)
		D-1	Dawson 1	42.9	0-85
2	1981. 5.26.	ES	Eshimashinriki	19.8	0-40
		N-61	Norin 61	18.1	0-40
3	1981. 8. 6.	N-8	Norin 8	41.4	0-70
		SB	Shirobozu	27.6	0-70
4	1981.11.19.	AB	Akabozu	24.4	0-65
		S-29	Saitama 29	22.4	0-65
5	1982. 5. 8.	AD	Akadaruma	22.4	0-70
		SD	Shirodaruma	20.7	0-70
6	1982.12.28.	B-1	Bezostaja 1	30.5	0-95
		F-1	Fultz 1	42.0	0-95
7	1982. 9.23.	HH	Haruhikari	30.0	0-40
		K-25	Konosu 25	12.7	0-40
		MQ	Marquis	38.9	0-40

1) Date when the plants were transferred into phytotron
2) Heading time of the plants sown in the field in the fall of 1982, represented as the number of days from March 31, 1983, to heading(1983.4.1.=1).
3) Minimum and maximum durations of chilling treatment applied

evaluating chilling requirement.

A container consisted of 11 rows with 12 plants each. In each treatment, 12 plants(one row) were allotted to a variety except in the 6th and 7th experiments, where 6 plants were assigned to a variety. There were no replications because a preliminary test had already shown no significant differences between the replications.

When the treatment duration was shorter than about 40 days, the 1st leaf unfolded after the treatment, but otherwise the 1st leaf unfolded within the period of the treatment, resulting in a negative value for Dt1. In such a case, the absolute value of Dt1 did not represent the number of days at 20°C (temperature after the treatment) but the number of days at 5°C (temperature during the treatment), which was much greater than that expected at 20°C, as shown in Fig. 3. Hence, for the estimation of the Dof suitable for the evaluation of chilling requirement, the observed Dt1 should be adjusted to the number of days expected at 20°C. The "adjusted Dt1" is represented in the following equation,

$$\text{Adjusted Dt1} = - B \times \text{Dt1}, \qquad \text{---(4)}$$

as B represents the ratio of the growth rate at 5°C to the growth rate at 20°C, as defined in Equation (1). There, B can be calculated using the data from the treatments in which all the 1st leaves unfolded after the treatment. For the treatments in which the 1st leaves unfolded within the period of the treatment, adjusted Dt1 was calculated according to Equation (4), then using the adjusted Dt1, Dof was evaluated based on Equations (2) and

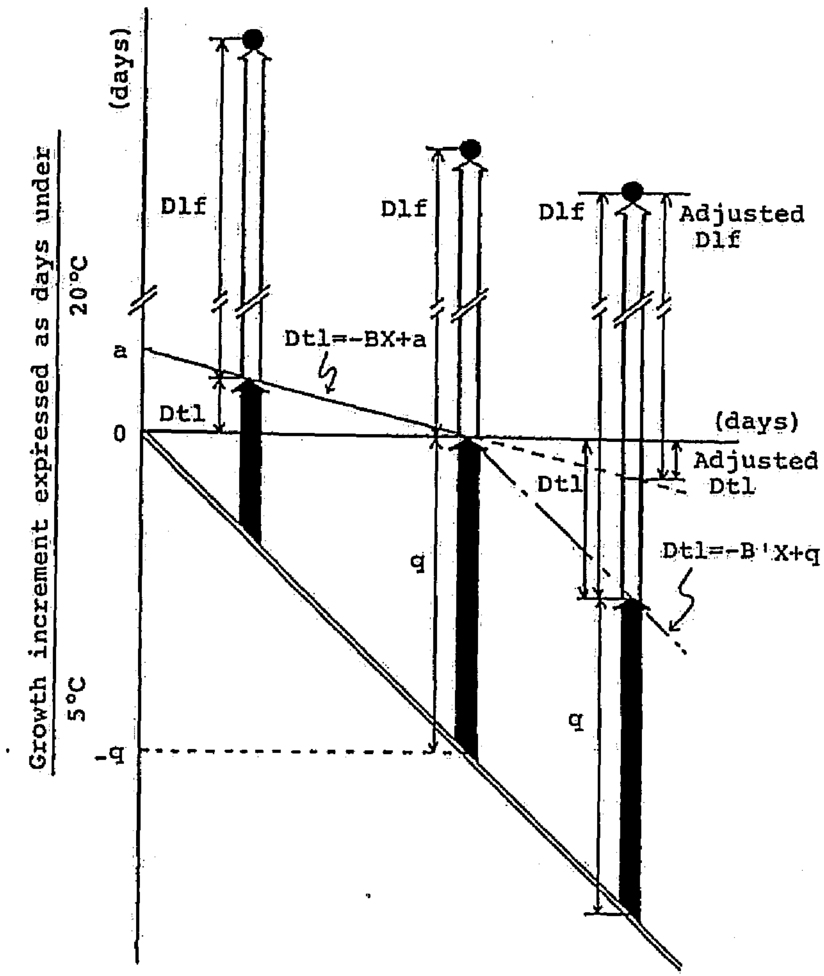

Fig. 3. Original and adjusted Dtl and Dlf of the plant whose 1st leaf unfolded within the period of the treatment.
Horizontal axis: Chilling treatment duration (in days)
Vertical axis: Growth increment expressed as number of days under 5°C(below 0) and 20°C(above 0). Zero refers to the end of chilling treatment. "a" and "q" represent the days required for the 1st leaf unfolding under 20°C and 5°C, respectively.
In the two equations, B(B') represents the ratio of growth rate at 5°C(5°C) to that at 20°C(5°C), hence B' is equal to 1.
=; Start of chilling treatment, ➡; Days from the start of chilling treatment (forced sprouting) to the 1st leaf unfolding, ●; Flag leaf unfolding

(3). Thus, hereafter in this paper, Dof as well as D1f will be expressed by the values modified by the adjusted Dt1.

Chilling requirement, i.e. the minimum duration (number of days) of the treatment necessary for full vernalization, was examined for each variety by successively testing the differences of the Dof between the treatments. The procedure used was as follows:

First, in all the treatments, the total N, was set in the ascending order of the length of duration, the longest being the (N)th treatment. Next, the difference of Dof between the (N)th and (N-1)th treatments was examined by t-test. When the difference was not significant($P>0.01$), the plants of the (N-1)th treatment were considered to be as fully vernalized as those of the (N)th treatment. Then, the same t-test was again applied to the difference between the (N-2)th treatment and the mixed population of the (N)th and (N-1)th treatments. When no significant difference was observed, the plants of the (N-2)th treatment were also considered to be as fully vernalized as those of the mixed population. In this way, the difference between the (M)th treatment and the mixed population composed of (M+1)th to (N)th treatments was successively examined until a significant difference ($P<0.01$) appeared. When a significant difference was detected, it was concluded that full vernalization was induced by (M+1 and more)th treatments, and that chilling requirement of the relevant variety could be represented by the duration of the (M+1)th treatment.

Results

In all the experiments and varieties, Dtl decreased linearly with the increase of the treatment duration, as reflected in the extremely high correlation coefficients ranged from r=-.961 to r=-.998 (Table 3). Figure 4 illustrates this linear relationship observed in the two winter wheat varieties used in Experiment 1, 'Akasabishirazu 1' and 'Dawson 1'. In this figure, Dtl's in 45 or more day treatments are represented by their adjusted values, since in these treatments the 1st leaves unfolded within the period of the treatment. According to the results of the t-test, the regression coefficients exhibited a significant difference among the seven experiments, but no varietal difference was detected in any of the experiments. These results support the assumption that the growth increment during the treatment increases linearly with the increase of the duration of the treatment (Fig. 1).

Table 4 and Fig. 5 present the relationship between Dof and the treatment duration for all the varieties examined and for the two varieties 'Akasabishirazu 1' and 'Dawson 1', respectively. Figure 5 also shows the relationship between Dtf and the treatment duration for comparison. Except for the three varieties 'Konosu 25', 'Marquis' and 'Fultz 1' (Table 4), Dof's maintained or reached the respective constant values with the increase of the treatment duration, whereas Dtf's showed a continuous decrease until the end. These results confirm the suitability of the plant-development model shown in Fig. 2.

In the two varieties shown in Fig. 5, for instance, the Dof

Table 3. Linear regression coefficient(b) of Dt1 on chilling treatment duration and correlation coefficient(r) between Dt1 and chilling treatment duration

Exp. No.	Variety	No. of treatments	b	a[1)]	r
1	ASS	14	-.174	8.09	-.997**
	D-1	14	-.186	8.23	-.997**
2	ES	9	-.106	6.19	-.995**
	N-61	9	-.101	6.76	-.989**
3	N-8	13	-.098	6.00	-.980**
	SB	13	-.105	6.07	-.980**
4	AB	13	-.142	8.11	-.994**
	S-29	13	-.142	7.61	-.992**
5	AD	13	-.137	6.56	-.993**
	SD	13	-.124	6.06	-.995**
6	B-1	14	-.155	7.04	-.998**
	F-1	14	-.157	7.38	-.997**
7	HH	9	-.219	6.95	-.986**
	K-25	9	-.215	6.91	-.981**
	MQ	9	-.215	6.86	-.984**

1) Intercept of linear regression equation
**; Significant at 1% level.

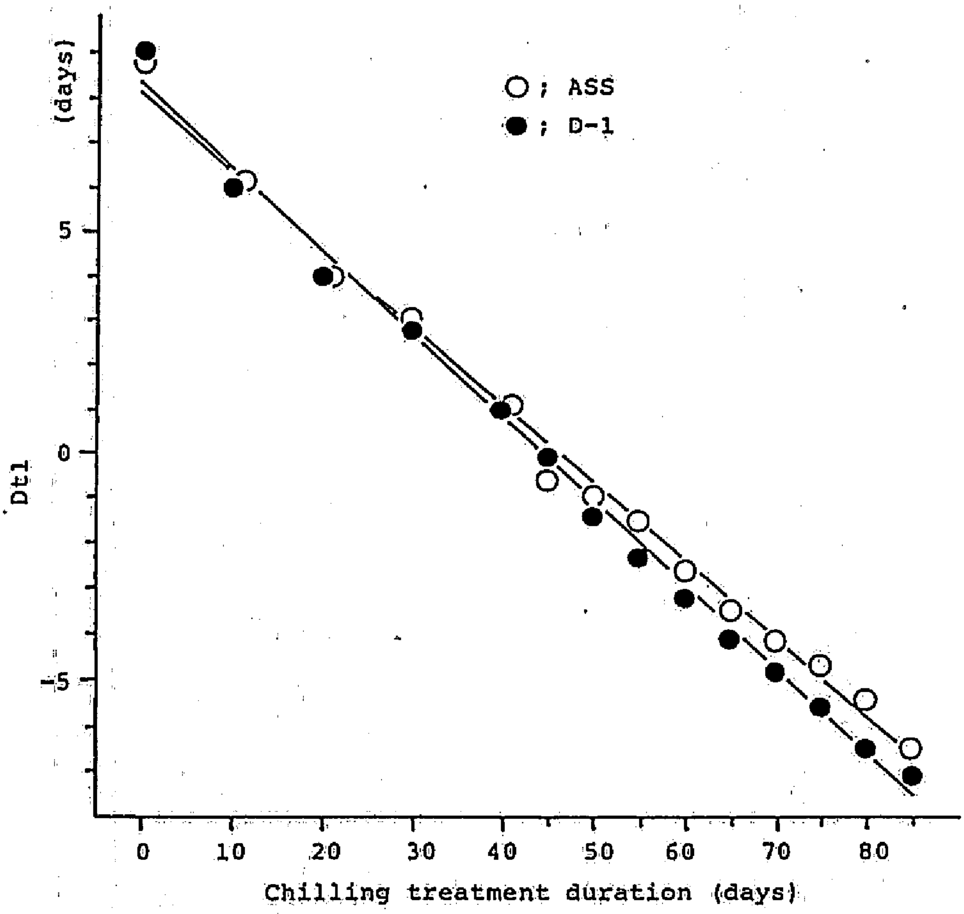

Fig. 4. Decrease of the number of days from the end of chilling treatment to the 1st leaf unfolding(Dt1) with the increase of chilling treatment duration.

Table 4. Change of the value of Dof with the increase of chilling treatment duration in 15 varieties

Treatment duration (days)	Variety														
	HH	K-25	MQ	ES	N-61	AB	S-29	AD	SD	N-8	SB	B-1	F-1	ASS	D-1
0	29.1*	26.6*	31.9*	32.3	29.7	38.4	x	x	x	x	x	x	x	x	x
5	29.1	26.1	30.4	30.5	29.3	-	-	-	-	-	-	x	x	-	-
10	29.9	26.3	30.6	30.1	28.4	33.2	65.4	x	x	x	x	-	-	x	x
15	28.7	25.9	30.0	28.2	27.0	31.3	52.8	-	-	-	-	x	x	-	-
20	29.0	25.9	30.1	25.8	25.7	30.1*	39.4	38.3	35.1	x	x	-	-	x	x
25	29.5	25.8	30.1	23.8	25.4	29.9	34.5	27.4	25.5	56.6	x	x	56.0	-	-
30	29.0	25.8	31.5	23.0*	24.2*	29.9	31.9	28.8	28.3	47.5	60.0	-	-	x	x
35	30.6	26.8	33.8	22.2	23.7	29.8	31.0	25.6	25.8	39.5	48.0	59.8	41.2	-	-
40	30.3	27.6	34.2	22.1	24.0	28.6	30.5	24.7*	22.8*	36.6	40.7	52.9	39.1	58.2	54.7
45	-	-	-	-	-	29.5	29.1	23.8	22.1	34.8	35.9	44.9	35.7	48.9	47.6
50	-	-	-	-	-	29.5	27.2*	24.5	22.1	29.8	31.2	41.5	35.0	42.4	43.1
55	-	-	-	-	-	28.6	27.0	24.2	22.4	28.5*	29.9	36.9	34.2	38.9	41.2
60	-	-	-	-	-	28.7	26.5	24.7	22.2	28.4	27.8*	34.3*	32.8*	37.5	40.6
65	-	-	-	-	-	27.5	26.8	24.0	22.2	28.1	27.0	33.5	32.7	36.1*	38.2*
70	-	-	-	-	-	-	-	24.7	22.1	27.3	26.5	-	-	36.5	39.1
75	-	-	-	-	-	-	-	-	-	-	-	32.9	34.3	36.0	39.5
80	-	-	-	-	-	-	-	-	-	-	-	-	-	35.8	38.6
85	-	-	-	-	-	-	-	-	-	-	-	34.0	38.9	36.0	39.0
90	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
95	-	-	-	-	-	-	-	-	-	-	-	34.9	39.9	-	-
Lowest value of Dof**	29.2	26.1	30.7	22.4	24.0	29.2	26.9	24.4	22.3	28.1	27.1	33.7	32.8	36.1	38.9

*; Indication of the treatment corresponding to chilling requirement (See the note on Table 5)
**; Mean Dof value among all the plants of the treatments which correspond to and longer than chilling requirement, except for K-25, MQ and F-1 as shown in text
-; No treatments were applied.
x; Treatment in which no flag leaves unfolded within the period of the experiments

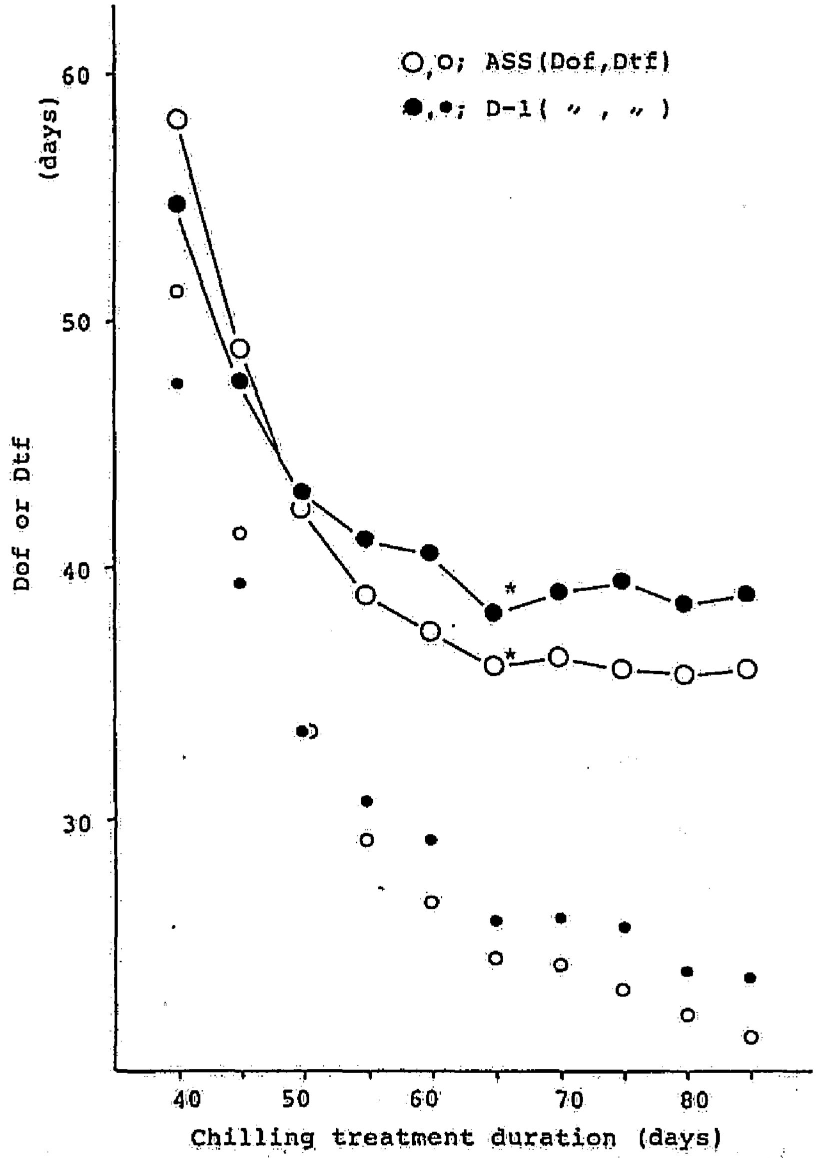

Fig. 5. Effects of chilling treatment on the number of days from the start of chilling treatment (forced sprouting) to flag leaf unfolding(Dof) and on the number of days from the end of chilling treatment to flag leaf unfolding(Dtf).
*; Indication of the treatment corresponding to chilling requirement

values became constant after 65 days of treatment. According to the model, this finding implies that these varieties were fully vernalized after treatments of 65 days and over, in other words, their chilling requirement is evaluated at 65 days. With the exception of the varieties 'Konosu 25', 'Marquis' and 'Fultz 1', whose Dof's finally increased with the increase of the treatment duration, chilling requirement was evaluated in the treatments where the increase of Dof did not yet appear.

Data on chilling requirement and narrow-sense earliness evaluated in the seven experiments are presented in Table 5, which shows that chilling requirement tended to increase with the degree of growth habit from grades I to VII. However, an inversion in chilling requirement occurred between a spring wheat variety 'Saitama 29'(III) and two winter wheat varieties 'Akadaruma'(IV) and 'Shirodaruma'(IV). Also among the spring wheat varieties, such an inversion was observed between a variety 'Akabozu'(III) and two varieties 'Eshimashinriki'(II) and 'Norin 61' (II). Moreover, chilling requirement of the IIa variety, 'Marquis', was estimated at 0 days. Thus, the magnitude of chilling requirement did not necessarily reflect the degree of growth habit.

As clearly seen in Table 4, all the varieties could be classified into two groups by the mode of flag leaf unfolding in the absence of chilling treatment: the varieties in which the unfolding occurred within 40 days, and those in which no unfolding occurred throughout the whole period of the experiments (ca. 70 days). Chilling requirement of the former ranged from 0

Table 5. Chilling requirement and narrow-sense earliness of 15 wheat varieties and their relation to the traits formerly evaluated

Variety	Chilling[1] requirement	Narrow-sense[2] earliness (Lowest value of Dof)	Growth[3] habit	Vernalization[4] requirement
HH	0 (days)	29.2 (days)	-	0 (days)
K-25	0	26.1	I	0
MQ	0	30.7	IIa	-
ES	30	22.4	II	0
N-61	30	24.0	II	0
AB	20	29.2	III	-
S-29	50	26.9	III	15
AD	40	24.4	IV	-
SD	40	22.3	IV	-
N-8	55	28.1	V	-
SB	60	27.1	V	-
B-1	60	33.7	-	60
F-1	60	32.8	VI	-
ASS	65	36.1	VII	60
D-1	65	38.9	VI	-

1) Minimum duration of chilling treatment necessary for full vernalization
2) Mean value of Dof of fully vernalized plants
3) Cited from KAKIZAKI and SUZUKI(1937).
4) Cited from GOTOH(1976).

to 30 days, while that of the latter from 40 to 65 days. In the latter, it was also observed that the minimum duration of the treatment necessary for flag leaf unfolding increased almost in parallel with the increase of chilling requirement, suggesting that chilling requirement corresponds well to the requirement of wheat varieties for a low temperature.

Data on narrow-sense earliness, the lowest values of Dof shown in Table 4, are presented in Table 5. A statistically significant difference was observed between varieties in each of the experiments except for the 6th one, indicating that there were varietal differences in narrow-sense earliness. The differences among the experiments, however, may not necessarily reflect substantial differences in narrow-sense earliness, because the growing environments, such as solar radiation, varied with the experiments.

Discussion

Evaluation of chilling requirement, i.e. the minimum duration of chilling treatment necessary for full vernalization, of a wheat variety requires a measurement which involves not only the growth after the treatment but also the growth during the treatment. Based on this concept, two assumptions for the growth during the treatment were proposed in this chapter, then an index Dof and a plant-development model using the Dof (Fig. 2) were developed on the basis of the assumptions. Throughout several experiments, the accuracy of the assumptions was clearly verified (Fig. 4 and Fig. 5), and the development model proved to be suitable for the evaluation of chilling requirement and narrow-sense earliness (Table 4 and Fig. 5).

1) Relationship between chilling requirement and other indices related to vernalization

The fifteen wheat varieties examined in this chapter could be classified into two groups of 6 and 9 varieties, based on whether flag leaf unfolding occurred or not in the absence of chilling treatment (Table 4). This classification revealed a distinct difference in chilling requirement between the two groups, the former being estimated at 0 to 30 days and the latter at 40 to 65 days (Table 5). Thus, the wheat varieties with a maximum of 30 days for chilling requirement and those with 40 or more days can be defined as spring wheat and winter wheat varieties, respectively.

Chilling requirement of a wheat variety has so far been estimated indirectly by the following three indices:

a) "Growth habit" represented by the latest sowing time which allows the variety to develop up to ear emergence under field condition (KAKIZAKI and SUZUKI 1937).
b) "Growth habit" represented by the duration from sowing to flag leaf unfolding under a 24h day-length regime without chilling treatment (YASUDA and SHIMOYAMA 1965; NAKAI and TSUNEWAKI 1967).
c) "Vernalization response" evaluated by the degree of the acceleration due to chilling treatment of the flag leaf unfolding under a 24h day-length regime (HALSE and WEIR

1970; PUGSLEY 1971; RAHMAN 1980; HOOGENDOORN 1984). These three indices are useful for a rough classification of wheat varieties into spring and winter wheat varieties, since they can be evaluated more readily than chilling requirement. Among them, growth habit defined by KAKIZAKI and SUZUKI (1937) is a useful index for practical breeding because it can be evaluated under field condition.

However, each of these indices represents only one of the responses of wheat to natural or artificial vernalization. Besides, growth habit defined by KAKIZAKI and SUZUKI (1937) is largely affected by photoperiodic response as indicated by YASUDA and SHIMOYAMA (1965). These facts may account for the reasons why chilling requirement and growth habit defined by KAKIZAKI and SUZUKI (1937) did not correspond to each other in the three varieties 'Marquis', 'Akabozu' and 'Saitama 29' (Table 5). 'Saitama 29' was formerly considered as a spring wheat variety due to the lower score (III) of growth habit (KAKIZAKI and SUZUKI 1937), but it was considered here as a winter wheat variety because chilling requirement exceeded 40 days (Table 5). GOTOH (1976) also reported that 'Saitama 29' was a winter wheat variety in terms of it's "vernalization requirement". A similar discrepancy in the evaluation has been revealed also in the variety 'Hayakomugi', one of the parents of 'Saitama 29' (KAKIZAKI and SUZUKI 1937; KATO and YAMAGATA unpublished). Thus, in some types of varieties such as 'Saitama 29' and 'Hayakomugi', it is impossible to estimate chilling requirement based on the growth habit only.

To estimate the low temperature requirement of wheat, GOTOH

(1976) attempted to evaluate vernalization requirement, an index expressed by the minimum duration of the treatment necessary for flag leaf unfolding within 34 days after the end of the chilling treatment. The values of this index, however, are larger than those of chilling requirement when varieties have a large narrow-sense earliness, and vice versa, because it is determined without considering the varietal difference in narrow-sense earliness. For instance, in the two spring wheat varieties with a small narrow-sense earliness, 'Eshimashinriki' and 'Norin 61', vernalization requirement (GOTOH 1976) was estimated at 0 days, while chilling requirement was estimated at 30 days (Table 5).

2) Chilling requirement and the genes responsible for chilling requirement

It is well known that the spring wheat varieties having Vrn1 do not require a low temperature for flag leaf unfolding. There are, however, discrepancies among the reports regarding the response of these varieties to chilling treatment, as some reports state that the varieties do not respond appreciably to chilling treatment (PUGSLEY 1971), while others state that they respond significantly to chilling treatment when they are fully vernalized by a treatment lasting for a maximum of 35 days (BERRY et al. 1980; FLOOD and HALLORAN 1984b). In the present study, however, the three varieties which had Vrn1, 'Konosu 25', 'Haruhikari' and 'Marquis' (Table 6), showed each a constant Dof value irrespective of the application or duration of the treatment (Table 4), indicating that these varieties did not

Table 6. Genotypes for chilling requirement of five spring wheat varieties

Variety	Genotype
Haruhikari (HH)	Vrn1 Vrn2 vrn3 vrn4
Konosu 25 (K-25)	Vrn1 vrn2 Vrn3 vrn4
Marquis (MQ)	Vrn1 vrn2 vrn3 vrn4
Eshimashinriki (ES)	vrn1 vrn2 Vrn3 vrn4
Norin 61 (N-61)	vrn1 vrn2 Vrn3 vrn4

Cited from GOTOH(1979a) and McINTOSH(1988).

respond to chilling treatment at all. This finding, therefore, suggests that the slight or drastic reduction in the number of days to flag leaf unfolding observed by PUGSLEY (1971), BERRY et al. (1980), and FLOOD and HALLORAN (1984b) is not due to vernalization by the treatment but to the growth during the treatment, and that Vrn1 makes wheat completely insensitive to chilling treatment.

It is well known that Vrn3 makes wheat slightly sensitive to chilling treatment (GOTOH 1979a). In the present study, chilling requirement of the two varieties having Vrn3 alone, 'Eshimashinriki' and 'Norin 61' (Table 6), was estimated at 30 days, as mentioned before. However, further analysis by using isogenic lines seems to be required for evaluating the magnitude of the action of Vrn3.

3) Narrow-sense earliness

YASUDA and SHIMOYAMA (1965) first succeeded in revealing the varietal difference of narrow-sense earliness in wheat based on the number of days from the end of the treatment to flag leaf unfolding under the optimum condition for reproductive growth. However, they did not evaluate narrow-sense earliness itself, because the growth during chilling treatment was not considered.

Recently, HOOGENDOORN (1984) estimated the growth increment during the treatment in terms of the number of primordia differentiated, and she suggested that narrow-sense earliness, "earliness per se" according to her, can be evaluated by adopting the growth increment as a component factor of plant development. Her concept, however, does not allow for the exact evaluation of narrow-sense earliness, because the authors consider that it is impossible to determine if the wheat plant has reached a fully vernalized state.

In contrast with these reports, the present study actually succeeded in revealing narrow-sense earliness of a given wheat variety. This may be exclusively due to the fact that the growth increment during the treatment and the fully vernalized state could be determined through the development model using the Dof index.

The accurate evaluation of chilling requirement by the use of the Dof index should contribute significantly to the elucidation of the nature and genetics of vernalization, because chilling requirement is not affected by narrow-sense earliness. The effect of the various factors related to vernalization, such as nuclear genes (KATO and YAMAGATA 1982; KATO and HAYASHI 1989), alien cytoplasms (KATO and YAMAGATA 1983; KATO and HAYASHI 1985) and chemical agents (KATO et al. 1990), has been successfully analyzed for their effect on chilling requirement, and the results may contribute to the breeding of heading time (NAGASAWA and TSUNEWAKI 1983) and to the shortening of the breeding cycle of wheat (BARBAS and CSEPELY 1978; KATO et al. 1990).

Summary

Chilling requirement, i.e. the minimum duration of the chilling treatment necessary for full vernalization, of a wheat variety/should be evaluated by using a measurement which involves not only the growth after the treatment but also the growth during the treatment. Based on this concept, two assumptions were proposed in this chapter for the growth during the chilling treatment. Subsequently an index 'Dof' and a plant-development model using the Dof (Fig. 2) were developed on the basis of the assumptions. Through a series of experiments involving 15 wheat varieties, the accuracy of the assumptions was verified, and the development model was found to be quite adequate for the evaluation of chilling requirement and narrow-sense earliness.

The fifteen wheat varieties examined in the present experiments were classified into two groups, i.e. spring and winter wheat varieties by the pattern of flag leaf unfolding in the absence of chilling treatment. This classification revealed a distinct difference in chilling requirement between the two groups, and enabled to conclude that the wheat varieties which required maximum of 30 days of chilling and those which required 40 or more days can be designated as spring wheat varieties and winter wheat varieties, respectively.

Among the spring wheat varieties, three that had Vrn1 and two having Vrn3 required a chilling treatment of 0 and 30 days for full vernalization, respectively. This finding indicates that Vrn1 makes wheat completely insensitive to chilling treatment and that chilling requirement controlled by Vrn3 disappears by 30 days of chilling treatment.

The experimental results showed that chilling requirement precisely reflects the demand of a wheat variety for low temperature for reproductive growth. Therefore, it is suggested that chilling requirement is the supremely important trait for understanding the nature and genetics of vernalization.

CHAPTER III. VARIETAL VARIATION IN PHOTOPERIODIC RESPONSE, CHILLING REQUIREMENT AND NARROW-SENSE EARLINESS AND THEIR RELATION TO HEADING TIME IN WHEAT

Introduction

Heading time of fall-sown wheat varieties is a complex character controlled by photoperiodic response, chilling requirement and narrow-sense earliness as mentioned in CHAPTER I. Among the three traits, according to EVANS et al. (1975), chilling requirement is an important trait for the adaptation to winter coldness and photoperiodic response for avoiding the damage caused by late frost. This fact indicates that the adaptability of wheat varieties should be improved more efficiently by taking the combination of the three heading traits into account for the breeding of heading time. The validity of such strategy was also pointed out by HASHIMOTO and HIRANO (1963), HUNT (1979), and YOSHIDA et al. (1983).

Precise evaluation of the three heading traits is prerequisite to take their combination into consideration. As to chilling requirement and narrow-sense earliness, evaluation method was established in CHAPTER I. Photoperiodic response has been measured as the difference in the number of days from the end of chilling treatment to flag leaf unfolding between short-day and long-day conditions (YASUDA and SHIMOYAMA 1965). On the other hand, it can also be measured as the ratio of such difference as proposed in barley by TAKAHASHI and YASUDA (1960). Although the difference between two measurements has never been analyzed, it must be confirmed which way of expression is suitable for precise evaluation of photoperiodic response.

According to SYME (1968) and LEVY and PETERSON (1972), heading time was mainly controlled by photoperiodic response and secondly by chilling requirement. The third factor, narrow-sense earliness, was ignored in both studies. The relationship between heading time and all of the three heading traits was first examined by YASUDA and SHIMOYAMA (1965). The most important factor in the control of heading time was photoperiodic response and the least was narrow-sense earliness. As they measured growth habit instead of chilling requirement, the effect of narrow-sense earliness was partly included in growth habit as pointed out in CHAPTER I, and thus was underestimated. HOOGENDOORN (1985a) also showed that narrow-sense earliness, as well as other two traits, could be exploited for the control of heading time. However, the relative importance of each trait was not statistically analyzed. It was suggested from these considerations that the obtained knowledge was not enough to know the effect of narrow-sense earliness on heading time.

In this study, therefore, photoperiodic response, chilling requirement, narrow-sense earliness and heading time were examined, using 158 wheat varieties. Their relationship was analyzed for investigating how these traits interacted to control the heading time. And the difference between the above-mentioned measurements of photoperiodic response was discussed.

Materials and Methods

To cover a wide range of varietal variation in each heading trait and in the combination of the three traits, 158 wheat landraces collected from various countries were examined. The detail of the landraces is shown in Tables 8, 12 and Fig. 11. Seeds of these varieties were supplied by the Plant Germ-plasm Institute, Kyoto University, Japan.

Chilling requirement was evaluated by the following way. Just sprouted seeds, which had been soaked on wet filter paper for 24 hours at 20°C, were put into a vernalization chamber under a 2°C and 24h day-length regime and kept for various periods ranged from 0 to 80 days at an interval of 10 days. Young seedlings were transplanted in small soil-filled containers at a spacing of 3cm (between hills) x 3cm (between rows), when the treatments were completed. The time of seed soaking was adjusted to the treatment duration so that all the treatments for each variety would be completed at the same time, in the middle of April. A container consisted of 12 rows with 12 plants each. In each variety, six plants (half row) were allotted to a treatment. Then they were grown in a glasshouse under a 24h day-length regime. The unfolding date of the 1st leaf and flag leaf was recorded, and the number of days from forced sprouting to flag leaf unfolding (Dof) was calculated. Chilling requirement was evaluated on the basis of the difference in Dof among chilling treatment durations. The detail of the evaluation method was fully described in CHAPTER I.

For the evaluation of narrow-sense earliness and photoperiodic response, just sprouted seeds of winter and spring wheat varieties were separately sown in different containers. The details of seed soaking, sowing density and so on were the same as in the experiment for chilling requirement, except that four plants were allotted to a treatment. As these two traits couldn't be measured unless the materials were fully vernalized, the containers with winter and spring wheat varieties were placed in a vernalization chamber, under a 5°C and 24h day-length regime, for 70 and 40 days, respectively. Then they were grown at 20°C in a growth chamber under 12h and 24h day-length regimes, and the unfolding date of flag leaf was recorded.

Narrow-sense earliness can't be exactly measured without the estimation of the amount of growth increment during chilling treatment. Such a growth increment was estimated by regression analysis of the number of days from forced sprouting to the 1st leaf unfolding, using chilling treatment duration as an independent variable as described in CHAPTER I. Near iso-genic lines of 'Triple Dirk', which differed in *Vrn* genotype, were also grown in vernalization chamber kept at 5°C for various periods ranged from 0 to 80 days at an interval of 5 days, and then grown in growth chamber kept at 20°C. Photoperiodic condition in both chambers was 24h day-length. The result showed that growth increment achieved in vernalization chamber for 70 and 40 days corresponded to growth increment achieved in growth chamber for 14.5 and 8.11 days, respectively. For the evaluation of narrow-sense earliness, therefore, the number of days from the end of chilling treatment to flag leaf unfolding under a 24h day-length regime was added with 8.11 days in spring wheat and with 14.5

days in winter wheat.

Photoperiodic response was measured as the difference in the growth period between day-length regimes and as the ratio of such a difference to the growth period under long-day condition. Growth period was measured as the number of days from forced sprouting to flag leaf unfolding (Dof).

Heading time was taken on one plant basis as the days from the 1st of April, using the materials sown in the experimental field of Kochi University (33°32'N,133°41'E, 7m above sea level) on the 15th of November in 1983. Ten plants were grown for each variety. Temperature condition during their growing season was given in Fig. 6, where daily temperature was recorded at 9 a.m..

Results

Figure 7 shows the change in Dof with the prolongation of chilling treatment duration in typical three wheat varieties. Two varieties, 'IL 120' and 'IL 182', unfolded flag leaf without chilling treatment, showing that these varieties were spring wheat. On the other hand, 'IL 91' failed to unfold flag leaf without chilling treatment and proved to be winter wheat. The result of t-test, which was performed after the method described in CHAPTER I, showed that Dof was not reduced by chilling treatment in 'IL 182'. In 'IL 120' and 'IL 91', it was reduced by chilling treatment and became constant by the treatment of more than 40 days and 60 days, respectively. Therefore, chilling requirement was evaluated at 0 days in 'IL 182', at 40 days in 'IL 120' and at 60 days in 'IL 91'.

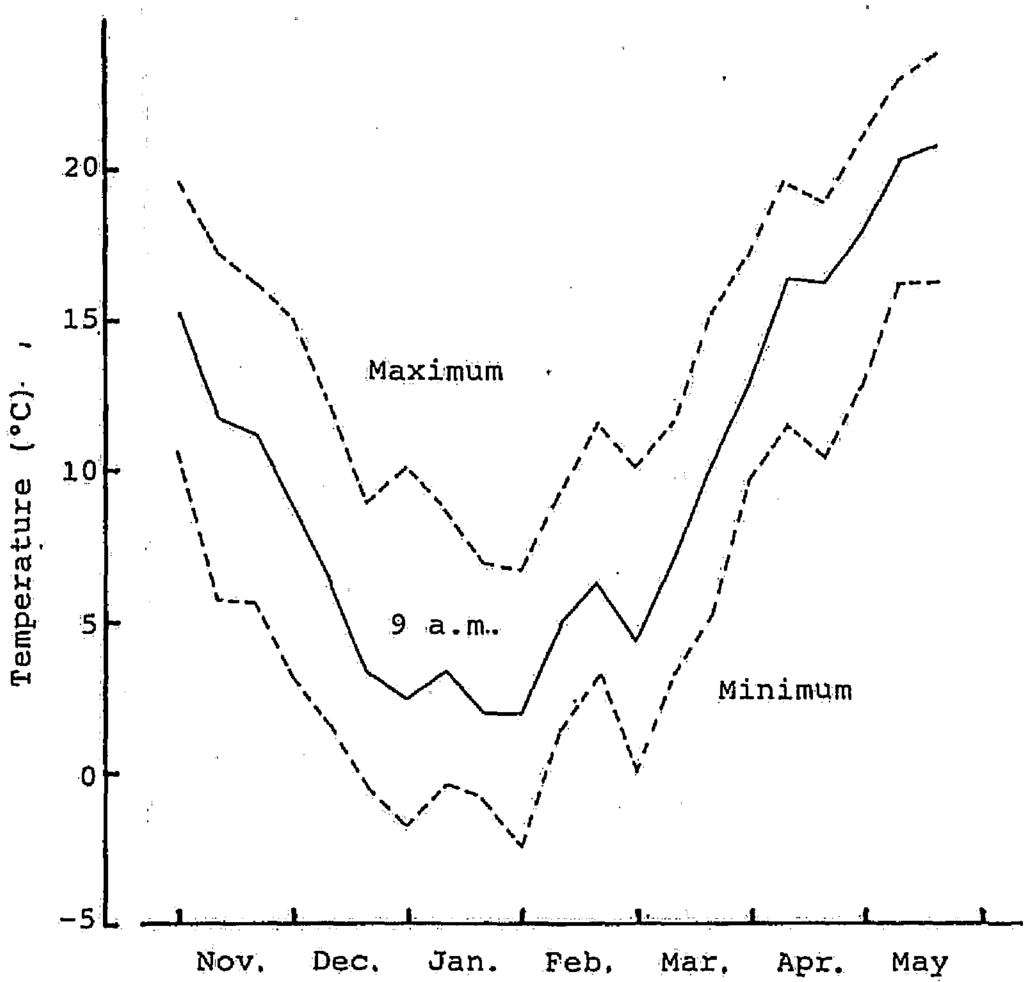

Fig. 6. Daily, maximum and minimum temperatures during wheat growing season, from November to May, at experimental field.
Temperatures were expressed as average for each one-third of a month.

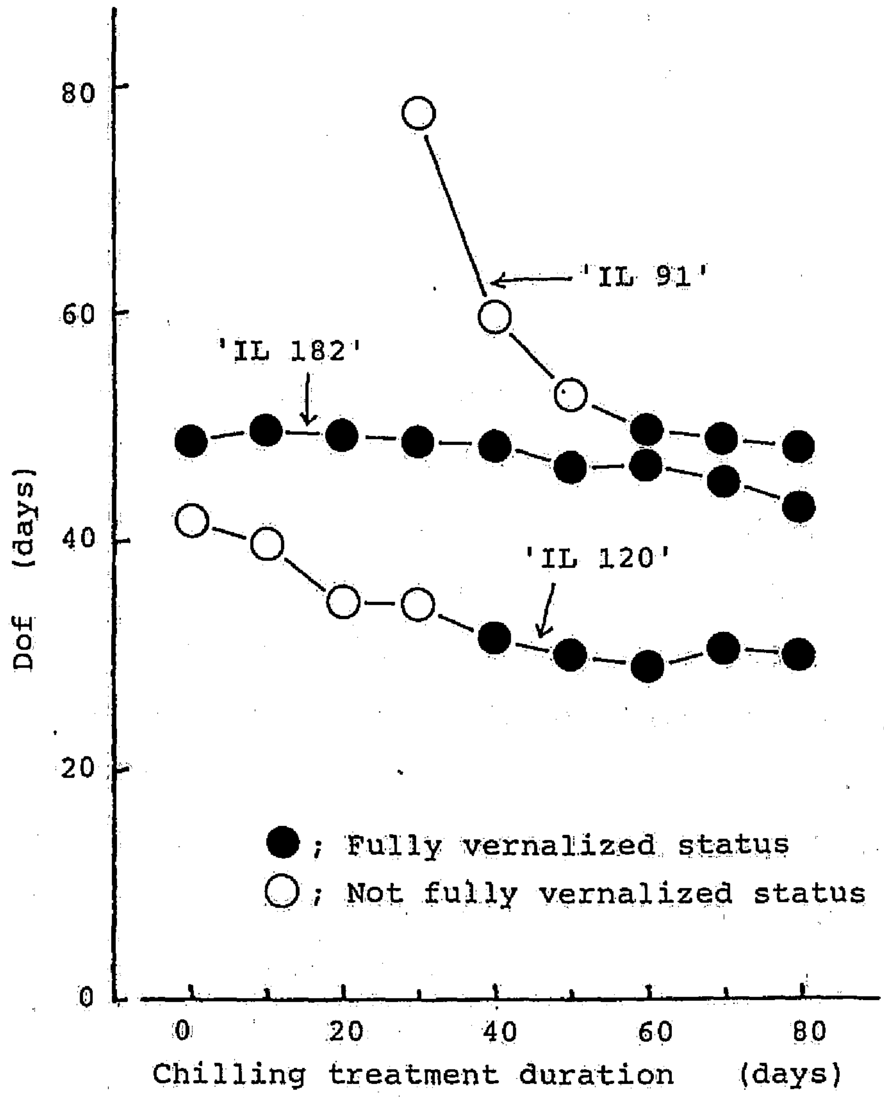

Fig. 7. Effect of chilling treatment on the number of days from forced sprouting to flag leaf unfolding (Dof) in three varieties, 'IL 91', 'IL 120' and 'IL 182'.

Chilling requirement of the other varieties was also evaluated in the same way. Frequency distribution of chilling requirement was shown in Fig. 8B, separately for spring and winter wheat varieties. Chilling requirement ranged from 0 days to 80 days, and differed clearly between spring and winter wheat varieties with one exception, being ranged from 0 days to 40 days in spring wheat and from 50 days to 80 days in winter wheat. Frequency distributions of heading time, narrow-sense earliness and photoperiodic response were also shown in Fig. 8. A wide varietal variation existed in each trait, from 13th of April to 18th of May in heading time (Fig. 8A) and from 27.6 days to 49.8 days in narrow-sense earliness (Fig. 8C). Photoperiodic response also showed wide varietal variation ranged from 10.3 days to 103.1 days in the difference (Fig. 8D) and from 1.30 to 3.51 in the ratio (Fig. 8E).

Correlation coefficients calculated between heading time and the three heading traits are shown in Table 7. Correlation coefficients between the three heading traits were all positive and statistically significant ($P<0.01$). Such relationship was consistently observed irrespective of the measurements of photoperiodic response, as two measures of photoperiodic response closely related with each other ($r=.977$, $P<0.01$). However, correlation coefficient between photoperiodic response and narrow-sense earliness was different between two measures of photoperiodic response ($P<0.05$), being lower in the ratio ($r=.588$, $P<0.01$) than in the difference ($r=.724$, $P<0.01$). This fact indicated that narrow-sense earliness partly influenced

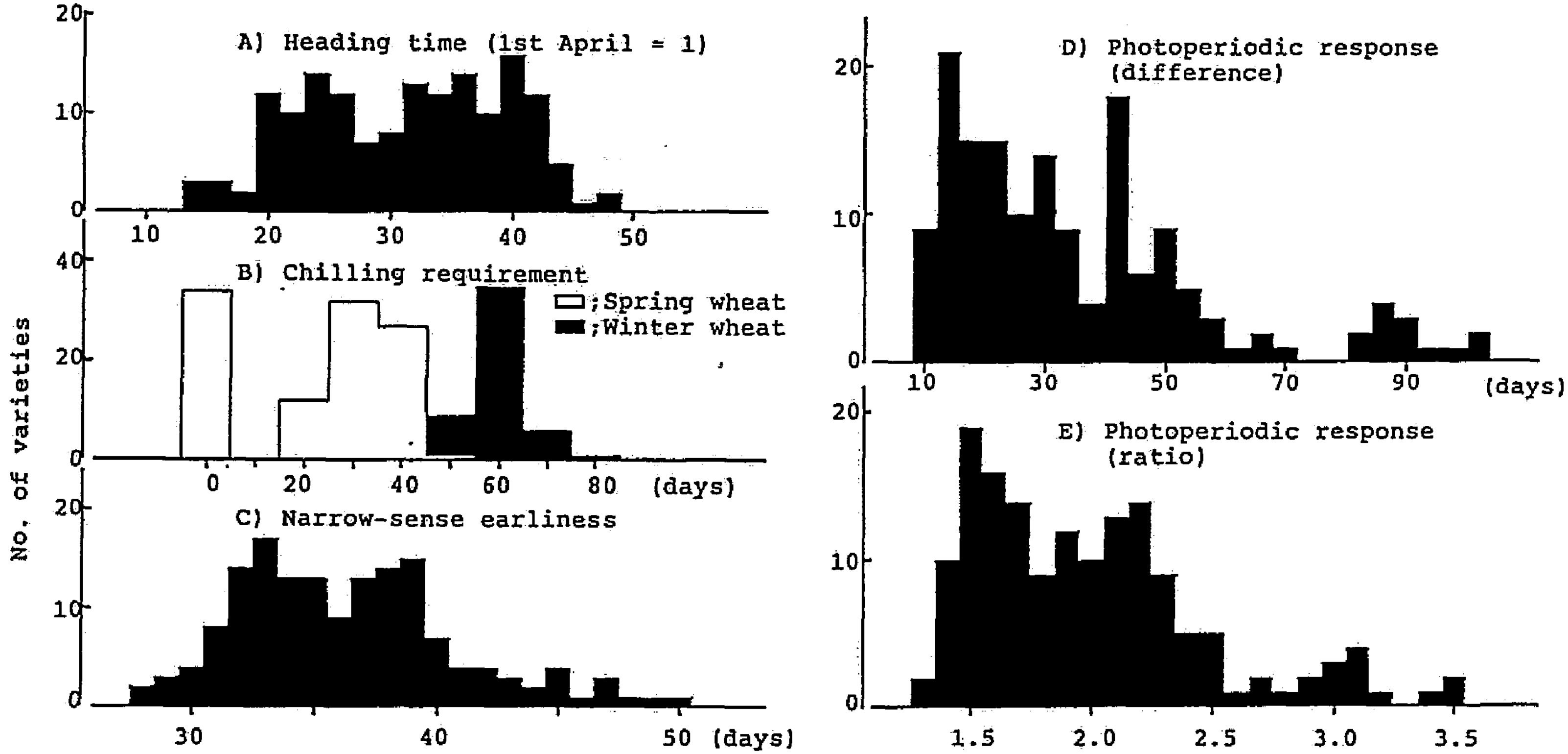

Fig. 8. Frequency distribution of heading time and three heading traits among 158 wheat varieties.
Photoperiodic response was measured as the difference and the ratio as described in the text.

Table 7. Correlation coefficient between heading time and three heading traits

	Chilling requirement (A)	Photoperiodic response (B)	Narrow-sense earliness (C)	Heading time: Simple correlation	Heading time: Partial correlation
difference[1]					
(A)	-	.402**	.562**	.475**	.114
(B)		-	.724**	.780**	.518**
(C)			-	.756**	.372**
ratio[1]					
(A)	-	.323**	.562**	.475**	.123
(B)		-	.588**	.752**	.584**
(C)			-	.756**	.503**

1) Photoperiodic response was measured as the difference and the ratio as shown in the text.
**; Significant at 1% level.

photoperiodic response measured as the difference, but not the one measured as the ratio. In this study, therefore, photoperiodic response is hereafter measured as the ratio of the growth period under short-day condition to the one under long-day condition.

Simple correlation coefficient calculated between heading time and chilling requirement was positive and statistically significant ($P<0.01$) as shown in Table 7. However, partial correlation coefficient was statistically insignificant, indicating that chilling requirement related indirectly with heading time. The positive correlation was due to the positive correlation between chilling requirement and the other traits closely related with heading time (Table 7). Spring wheat varieties showed a wide varietal variation in heading time as shown in Fig. 9, and most of winter wheat varieties were late in heading time. Such relationship might make their simple correlation coefficient statistically significant. However, almost whole variation in heading time was covered by the varieties whose chilling requirement was estimated at 0 days, clearly indicating the independence of heading time from chilling requirement.

Photoperiodic response and narrow-sense earliness closely related with heading time as shown in Table 7 and Fig. 10. Partial correlation coefficients of these two traits on heading time were statistically significant ($P<0.01$), indicating that both traits were important in the control of heading time. It was also indicated that narrow-sense earliness was important as well as photoperiodic response. The result of multiple

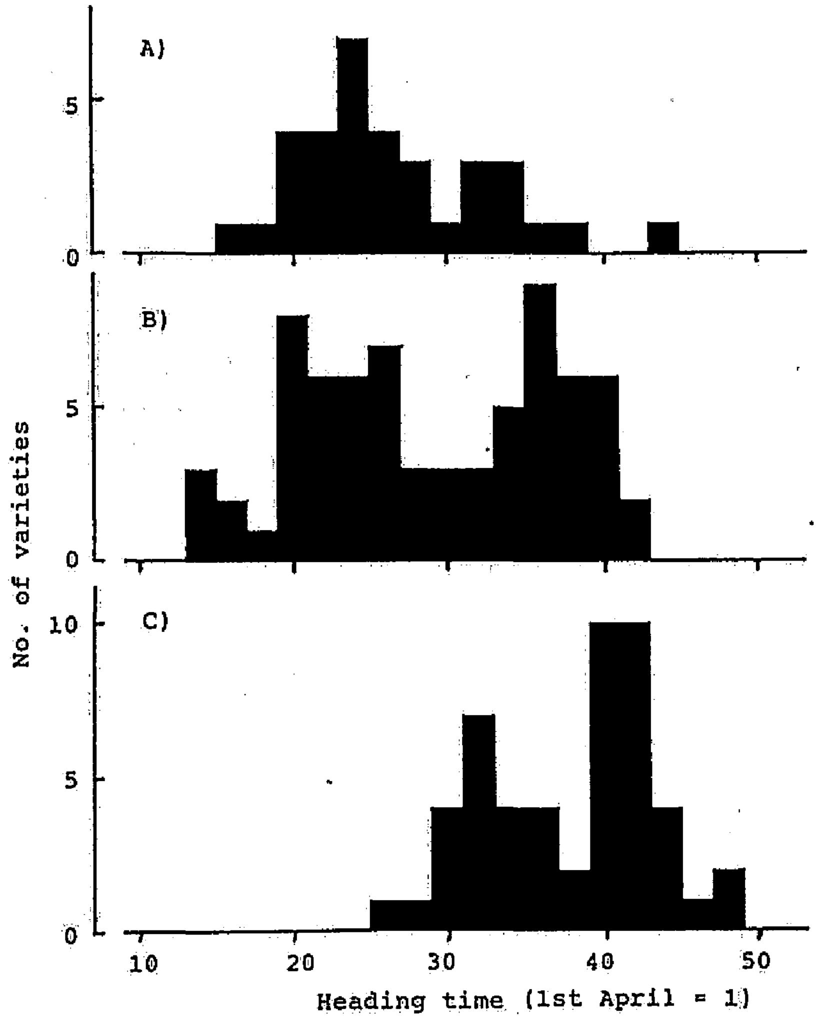

Fig. 9. Varietal variation in heading time among wheat varieties belonging to respective chilling requirement class.
A) 0 days, B) 20-40 days, C) 50-80 days

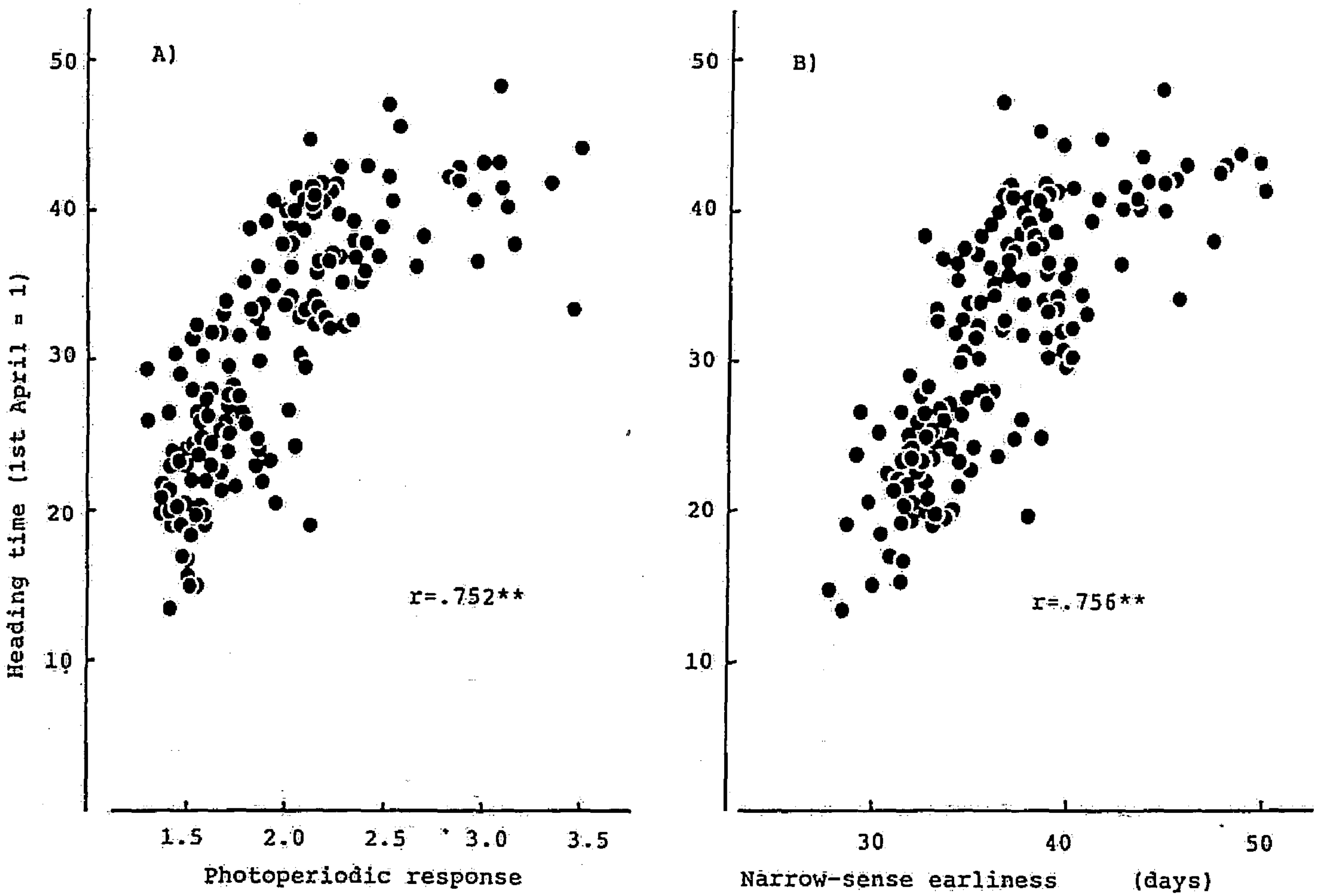

Fig. 10. Relation of photoperiodic response (A) and narrow-sense earliness (B) to heading time among 158 wheat varieties.
**; Significant at 1% level.

regression analysis revealed that about 85% of whole variation in heading time could be explained by these two traits.

Discussion

As artificially bred varieties generally possess narrow genetic variation, landraces seem to be suitable for investigating the relationship between heading time and the three heading traits. However, even in landraces, genetic variation in heading time and the three traits might be poor within the same collection site, because heading characters are adaptatively important and severely subjected to natural and artificial selection (RAO and WITCOMBE 1977). In this study, as the varieties tested had been cultivated under diverse growing environments (Table 8 and Fig. 11), a wide varietal variation was observed in the combination of the three heading traits as well as in each trait itself. This result indicated that these varieties were suitable for analyzing the relationship between heading time and the three heading traits.

Photoperiodic response and narrow-sense earliness were genetically independent with each other, as clearly indicated from the fact that the former was controlled by Ppd genes (PUGSLEY 1965; KEIM et al. 1973; SCARTH and LAW 1983) and the latter by polygenes (KATO et al. 1989). Therefore, the correlation coefficient between these two traits should be lowered by the increase in precision in measuring each trait, and finally reach a certain level. By measuring photoperiodic response as the ratio, in this chapter, correlation coefficient between these two traits was lowered (Table 7) and the difference was statistically significant ($P<0.05$). This result indicated that photoperiodic response measured as the difference was partly influenced by narrow-sense earliness, and that the effect of narrow-sense earliness could be neglected by measuring photoperiodic response as the ratio. It was concluded from these considerations that photoperiodic response should be measured as the ratio of the growth period under short-day condition to the one under long-day condition.

The relationship between heading time and the three heading traits largely depends on growing environments as shown by SYME (1968). YASUDA and SHIMOYAMA (1965) and CHO et al. (1983) investigated the relationship in fall-sowing area in temperate zone, thus these results should be comparable to the result of this chapter. Although similar tendency was observed in simple correlation coefficient as compared with those reports, partial correlation coefficient showed different tendency, being higher in narrow-sense earliness and lower in chilling requirement. Such a difference seemed to be caused by the improvement of precision in measuring each trait. In this chapter, chilling requirement defined in CHAPTER I was measured instead of growth habit, and photoperiodic response was measured as the ratio as mentioned above. These measurements were not distorted by narrow-sense earliness and made it possible to draw the following conclusions. (1)Chilling requirement does not influence the control of heading time (Table 7 and Fig. 9). (2)Narrow-sense earliness, whose importance was underestimated in the former reports, proved to be as important as photoperiodic response (Table 7 and Fig. 10).

HASHIMOTO and HIRANO (1963), GOTOH (1975), and YASUDA (1984) investigated the completion date of vernalization in the field in different parts of Japan. Although temperature condition in the winter and tested varieties were different between these reports, vernalization completed by the end of January in all varieties including winter wheat varieties. KIRBY et al. (1985) and GEORGE (1982) also reported that, even in winter wheat varieties, initiation of spikelet primordium began by November in UK and by late January in Washington, USA, respectively. These results indicated that even winter wheat varieties were fully vernalized in the field in the winter. However, initiation of spikelet primordium did not occur during the cold winter (YASUDA 1984). These informations led to the assumption that lag phase should exist between the two events, namely, completion of vernalization and initiation of spikelet primordium. The timing of the former is of course influenced by chilling requirement, but the timing of the latter and thus heading time is not necessarily affected by chilling requirement. It was concluded that, in fall-sowing areas in temperate zone, chilling requirement was not important in the control of heading time, but for the adaptation to winter coldness. The independence of heading time from chilling requirement was demonstrated also in the breeding programme for early heading varieties (HASHIMOTO and HIRANO 1963). On the other hand, in spring-sowing (MASLE et al. 1989), in summer-sowing (KATO and SHIGENAGA 1981), in the mild winter (GOTOH

1979b), and in tropical area (LEVY and PETERSON 1972; WALL and CARTWRIGHT 1974), chilling requirement does influence heading time through the retardation of heading in insufficiently vernalized varieties.

Narrow-sense earliness proved to be as important in the control of heading time as photoperiodic response. However, the mechanism to control heading time is considered to be different between these two traits. As stated by LEVY and PETERSON (1972), it is well recognized that heading occurs on the same calendar date every year in a variety whose heading time is mainly controlled by photoperiodic response. On the other hand, narrow-sense earliness might be regarded as the requirement of cumulative temperature necessary for growing up to heading stage as suggested by MASLE et al. (1989). Therefore, heading time should be controlled by narrow-sense earliness so that a certain level of vegetative growth can be assured, though heading time may vary from year to year. Early heading in cold year/place and late heading in hot year/place should be also avoided to ensure normal fertility and grain filling. These considerations suggested that heading time of wheat variety can be well adjusted to its growing environment by combining these two traits. However, as little is known about their influences on wheat adaptation, further study is necessary to know the best strategy for wheat breeding at diverse areas.

Summary

Heading time of fall-sown common wheat varieties and the three

heading traits, i.e. photoperiodic response, chilling requirement and narrow-sense earliness, were examined, using 158 wheat landraces collected from various countries. And their relationship was analyzed for investigating how these traits interacted to control heading time. A wide varietal variation was observed in each heading trait as well as in heading time itself. Correlation coefficient between narrow-sense earliness and two measures of photoperiodic response, which was calculated as the difference in or as the ratio of the growth period under long-day and short-day conditions, was higher in the former ($r=.724$) than in the latter ($r=.588$). The existence of such difference ($P<0.05$) indicated that photoperiodic response measured as the difference partly included the effect of narrow-sense earliness, and that photoperiodic response should be measured as the ratio. Although simple correlation coefficient calculated between heading time and chilling requirement was positive and statistically significant ($P<0.01$), partial correlation coefficient was statistically insignificant. In addition, almost whole variation in heading time was covered by the varieties whose chilling requirement was estimated at 0 days. These facts clearly indicated that chilling requirement was not important in the control of heading time, but for the adaptation to winter coldness. On the other hand, partial correlation coefficients of photoperiodic response and narrow-sense earliness on heading time were statistically significant ($P<0.01$), indicating that both traits influenced the control of heading time. It was also concluded that narrow-sense earliness was as important in the control of heading time as photoperiodic response, though this trait was formerly considered as a minor factor. And the mechanism to control heading time seemed to be different between these two traits. Therefore, narrow-sense earliness as well as photoperiodic response should be taken into account for the breeding of heading time in wheat.

CHAPTER IV. GEOGRAPHICAL VARIATION IN HEADING CHARACTERS AMONG WHEAT LANDRACES AND ITS IMPLICATION FOR THEIR ADAPTABILITY

Introduction

Landraces are regarded as an important gene pool for crop improvement (HARLAN 1975). To utilize these efficiently, primary information on their agronomic traits is a prerequisite. In cultivated wheat, extensive surveys have concentrated on several traits, such as morphological and metrical characters (WITCOMBE and RAO 1976; POIARKOVA and BLUM 1983; BEKELE 1984; YILMAZ and TAHIR 1988; EHDAIE and WAINES 1989). Less attention has so far been paid to developmental characters, though adaptability of wheat varieties is largely affected by such characters.

As one of the primary developmental characters, heading time has been surveyed in hexaploid wheat (JARADAT 1991) and in tetraploid wheat (QUALSET and PURI 1974), and shows wide variation among landraces and areas of their origin. However, heading time is evaluated in the field and thus varies depending on the growing environments. However, the three heading traits, namely, photoperiodic response, narrow-sense earliness and chilling requirement are intrinsic characters of each landrace and can be evaluated under controlled environment. As described in CHAPTER III, in the south-western part of Japan, about 85% of varietal variation in heading time of fall-sown wheat varieties could be explained by the difference in photoperiodic response and narrow-sense earliness. These facts indicate that, once the relationship between heading time and the three heading traits is established for each area, heading time can be roughly estimated on the basis of the three heading traits. In addition, the breeding of heading time seemed to become more efficiently by selecting individual traits rather than the combined product, namely, heading time itself (HASHIMOTO and HIRANO 1963; HUNT 1979; YOSHIDA et al. 1983). For efficient utilization of wheat landraces, therefore, each trait should be surveyed as well as heading time itself. Additionally, geographical aspects of variation patterns must be also revealed to collect wheat germplasm efficiently (MURPHY and WITCOMBE 1981).

By the analysis of geographical diversity in heading characters, adaptation strategy to diverse growing environments through the adjustment of heading time should be explainable in terms of the combination of the three heading traits. This relationship has been analyzed for many improved varieties (HOOGENDOORN 1985b). However, they may have lost genes adapted to the local environments, through outbreeding with foreign varieties. On the contrary, characteristically adapted genotypes of each area should be found in landrace. Accordingly, a study of landraces should lead to the understanding of adaptation strategy to each growing environment.

Variability in adaptive characters is related to environmental heterogeneity (MURPHY and WITCOMBE 1981), though the center of diversity in qualitative characters corresponds to the center of crop evolution. In this chapter, therefore, heading time and the three heading traits were surveyed for wheat landraces not only in the center of wheat evolution but also in neighboring areas. The adaptation strategy in each area is discussed in relation to the prevailing environment.

Materials and Methods

The experimental data obtained in CHAPTER III was again analyzed from another stand point in this chapter. Accordingly, the experimental materials are 158 wheat landraces collected from various countries (Table 8), to cover a wide range of variation in the combination of the three heading traits as well as in each trait itself. Landraces were grouped into thirteen localities as shown in Table 12 and Fig. 11, according to their geographical origins and the growing environments. These localities were again grouped into 4 regions as shown in Table 12. The collection site of each landrace is fully described by TANAKA (1983). Six improved varieties were also used as check varieties, representing two distinct types for heading time in the field (Table 9). Spring wheat varieties of North American origin were also compared.

The method to measure heading time and the three heading traits are fully described in CHAPTER III.

The frequency distribution, mean and variance were calculated for each character for each region or locality. Differences in mean and variance among regions or localities were tested for significance by using F-tests. By an analysis of variance, the total variance of each character was divided into components due to differences among regions, among localities within regions and

Table 8. Cultivated area and number of varieties examined in this chapter

Cultivated area	No. of varieties	Cultivated area	No. of varieties
Bhutan	10	Georgia (USSR)	10
Nepal	13	Armenia (USSR)	9
Pakistan	10	Greece, Italy	5
Afghanistan	20	Iraq	5
Iran	29	Egypt	5
Turkey	19	Ethiopia	23

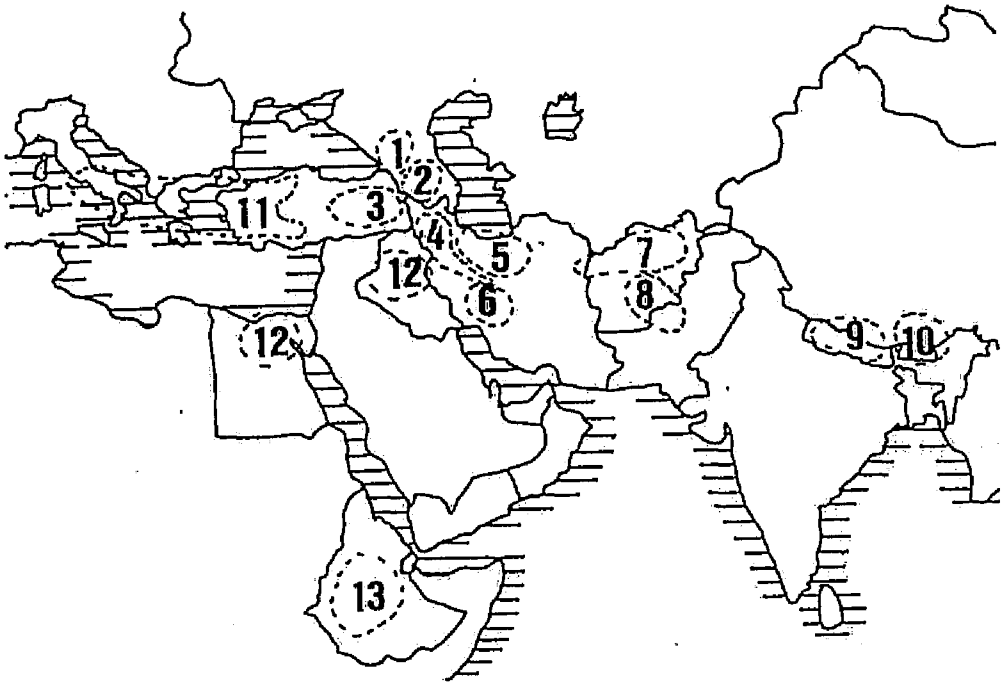

Fig. 11. Geographical distribution of localities where wheat landraces were collected.
Numerical characters represent locality No. shown in Table 12.

among landraces within localities. Simple correlation coefficients were calculated between heading time and the three heading traits for each locality.

Climatic data was taken from HATAKEYAMA (1964) and "Climatic Table for the World" published by the Japan Meteorological Agency. The name of the nearest representative city, where climatic data was recorded, is mostly shown for each locality in Table 14. As to the other localities, it was as follows: Tbilisi (Georgia), Rasht (Iran-east), Katmandu (Nepal), and Bursa (the Western Region). Bhutan and Ethiopia were excluded because of lack of climatic data and of completely different growing environments, respectively.

Results

Frequency distributions for each character are shown for each region in Fig. 12A-D. Varietal variation for each character was clear as compared with check varieties (Table 9), despite no landrace heading earlier than early Japanese varieties. Estimation of the variance components revealed that more than 50% of total variance was ascribable to varietal differences within localities for all characters, followed by the component due to the difference among regions (Table 10). Variance components due to the difference among localities within regions were the least among the three components for all characters, justifying the adequacy of grouping of localities into regions.

The mean and standard deviation of each character is shown for each region in Table 11. Differences in mean value among regions

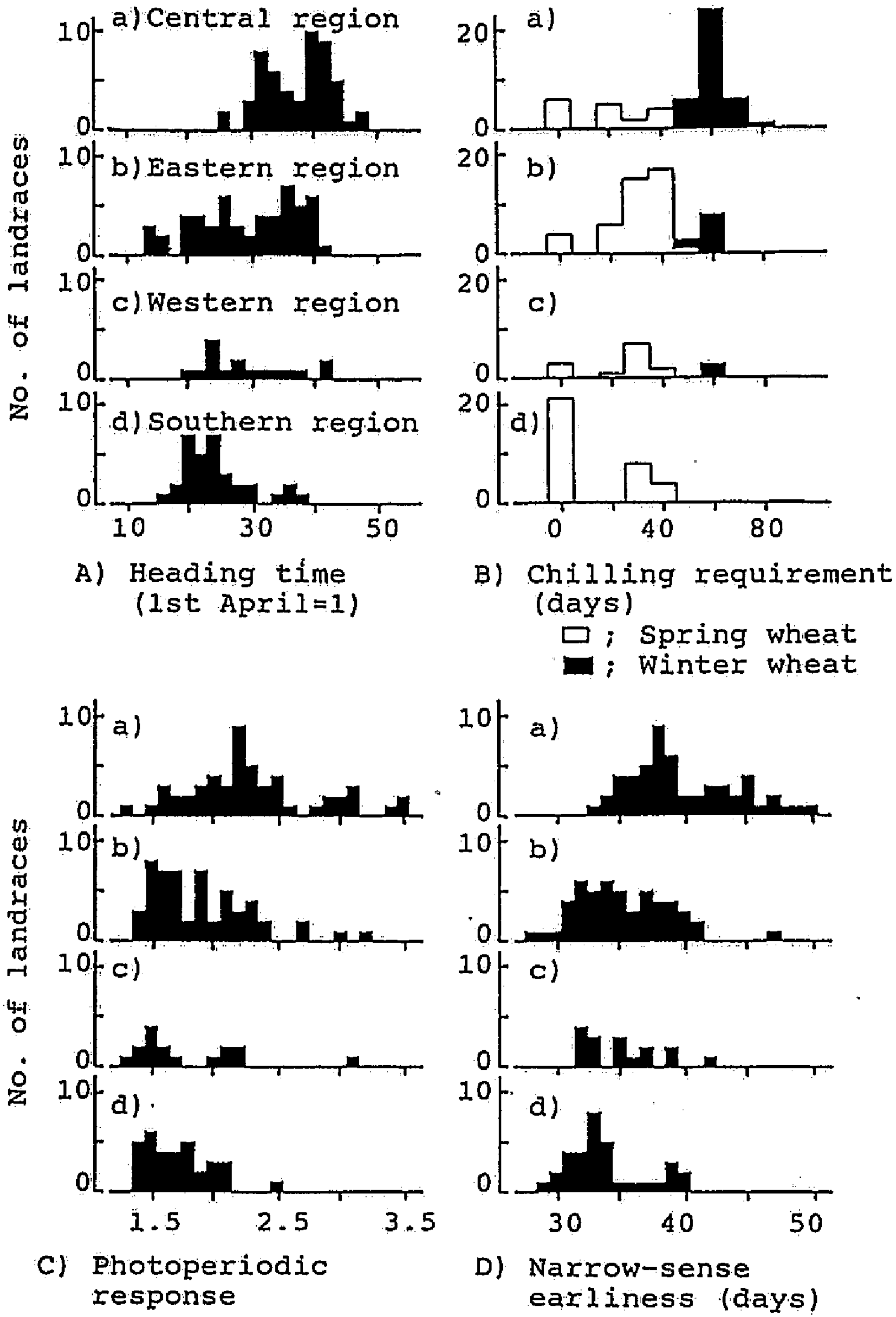

Fig. 12. Frequency distribution of heading time and three heading traits for wheat landraces in each region.

Table 9. Mean heading time and three heading traits for Japanese and North American wheat varieties

Variety	Heading time	Chilling requirement (days)	Photoperiodic response	Narrow-sense earliness (days)
Japan				
Gokuwase 2	8.8	30	1.18	32.5
Chugoku 114	11.0	30	1.12	32.0
Konosu 25	14.2	0	1.37	32.0
North America				
Baart	29.3	0	1.86	36.6
Ceres	30.9	0	2.22	35.9
Cadet	36.0	0	2.03	38.1

Table 10. Variance components (% phenotypic variance) due to regional effect, local effect and differences among landraces within localities

Character	Between regions	Between localities within regions	Within localities	Total
Heading time	42.0 %	5.9 %	52.1 %	100 %
Chilling requirement	36.1	7.7	56.2	100
Photoperiodic response	23.9	13.7	62.4	100
Narrow-sense earliness	37.2	6.7	56.1	100

Table 11. Mean and standard deviation of heading time and three heading traits for wheat landraces from each region

Region	Number of landraces	Heading time	Chilling requirement (days)	Photoperiodic response	Narrow-sense earliness (days)
Central region	54	37.8±5.26	47.4±22.2	2.31±0.513	40.1±4.25
Eastern region	55	29.8±8.13	35.5±15.6	1.91±0.401	35.0±3.85
Western region	16	29.5±6.97	30.6±19.5	1.79±0.459	35.2±3.13
Southern region	33	24.6±5.29	12.1±16.5	1.71±0.267	33.8±3.03
Total	158	31.4±8.23	34.2±22.6	1.99±0.485	36.5±4.58
LSD ($P<0.01$)		1.95	5.54	0.13	1.12
Difference in variance		**	*	**	*

*,**; Significant at 5% and 1% level, respectively.

were statistically significant for each character ($P<0.01$). Landraces in the Central Region generally exhibited the largest values for the three heading traits, and thus became late in heading time. Conversely, landraces in the other regions showed relatively early heading, being earliest in the Southern Region. Two types of clinal pattern in geographical difference were clearly demonstrated in Fig. 12. In heading time and narrow-sense earliness, landraces were concentrated in the medium or late classes in the Central Region, while the frequency of late types decreased and early types, which were absent in the Central Region, appeared in the other regions, especially in the Eastern (Nepal and Bhutan) and the Southern Regions (Fig. 12A,D). In chilling requirement and photoperiodic response, a whole range of varietal variation was covered by landraces in the Central Region (Fig. 12B,C). As compared with the Central Region, the relative frequency of sensitive and insensitive types changed in the other regions, resulting in a weaker response both to low temperature and to photoperiod (Table 11). Such a clinal pattern was clearly demonstrated in chilling requirement. In the Central Region, the whole range of variation from 0 days to 80 days was covered and the frequency of winter wheat was 67%. It decreased to about 20% in the Eastern and the Western Regions, and to 0% in the Southern Region. Furthermore, the frequency of highly spring type increased to 63% in the Southern Region.

Differences in variance among regions were examined by the F-test, comparing the minimum and the maximum variances. As shown in Table 11, it proved to be statistically significant for all characters. In heading time, variance was largest in the Eastern

Region and least in the Central Region. On the contrary, for the three heading traits, it was largest in the Central Region.

Differences among localities for each character were also statistically significant ($P<0.01$) as shown in Table 12. Although the number of landraces in each locality was relatively small, differences were clearly demonstrated even among neighboring localities. Landraces from the southern part of Iran exhibited smaller values in the three heading traits and thus were earlier in heading time than the ones from the northern part of Iran. Similar differences were observed between the northern and the southern parts of Afghanistan (plus Pakistan in Table 12).

Correlation coefficients between heading time and the three heading traits were calculated for each locality and are summarized in Table 13. Correlations with chilling requirement were not statistically significant in all localities with one exception, indicating that chilling requirement did not influence the control of heading time. Photoperiodic response and narrow-sense earliness showed a similar trend with their relationship to heading time, being different among regions or localities. In the Central Region, the correlation coefficient was statistically insignificant in most localities. Figure 13 shows the relative contributions of these two traits to heading time for landraces from the northern part of Iran, expressed as a multiple product of standardized data of each landrace and standardized partial regression coefficient of each trait on heading time. As clearly shown in this figure, the factor(s) causing late heading was

Table 12. Number of landraces examined and mean heading time and three heading traits in each region

No.	Locality	Number of landraces	Heading time	Chilling requirement (days)	Photoperiodic response	Narrow-sense earliness (days)
	Central region					
1	Georgia (USSR)	10	36.7	58.0	2.18	40.1
2	Armenia (USSR)	9	38.3	27.8	2.21	38.1
3	Turkey (East)	8	40.9	52.5	2.26	40.5
4	Iran (North)	13	40.5	51.5	2.71	43.3
5	Iran (East)	5	37.4	60.0	2.43	38.6
6	Iran (South)	9	32.5	37.8	1.88	38.0
	Eastern region					
7	Afghan (North)	17	33.3	37.7	2.09	36.2
8	Afghan (South), Pakistan	15	28.1	34.3	1.89	34.8
9	Nepal	13	29.4	35.4	1.83	34.9
10	Bhutan	10	26.6	33.3	1.74	33.3
	Western region					
11	Turkey (West), Italy and Greece	16	29.5	30.6	1.79	35.2
	Southern region					
12	Egypt, Iraq	10	23.1	7.0	1.72	33.3
13	Ethiopia	23	25.2	14.4	1.71	34.0
	LSD (P<0.01)	-	1.88	5.32	0.12	1.08

Table 13. Correlation coefficients between three heading traits and heading time in the field

No.	Locality	Chilling requirement	Photoperiodic response	Narrow-sense earliness
	Central region			
1	Georgia (USSR)	-.049	.927**	.522
2	Armenia (USSR)	.234	.502	.371
3	Turkey (East)	.742	.880**	.756*
4	Iran (North)	.433	.283	.522
5	Iran (East)	.159	.513	.758
6	Iran (South)	.550	.578	.439
	Eastern region			
7	Afghan (North)	.216	.686**	.830**
8	Afghan (South), Pakistan	.631*	.665**	.632*
9	Nepal	.195	.832**	.833**
10	Bhutan	-.268	.977**	.873**
11	Western region	.435	.737**	.734**
	Southern region			
12	Egypt, Iraq	.503	.180	.620
13	Ethiopia	-.177	.850**	.518*

*,**; Significant at 5% and 1% level, respectively.

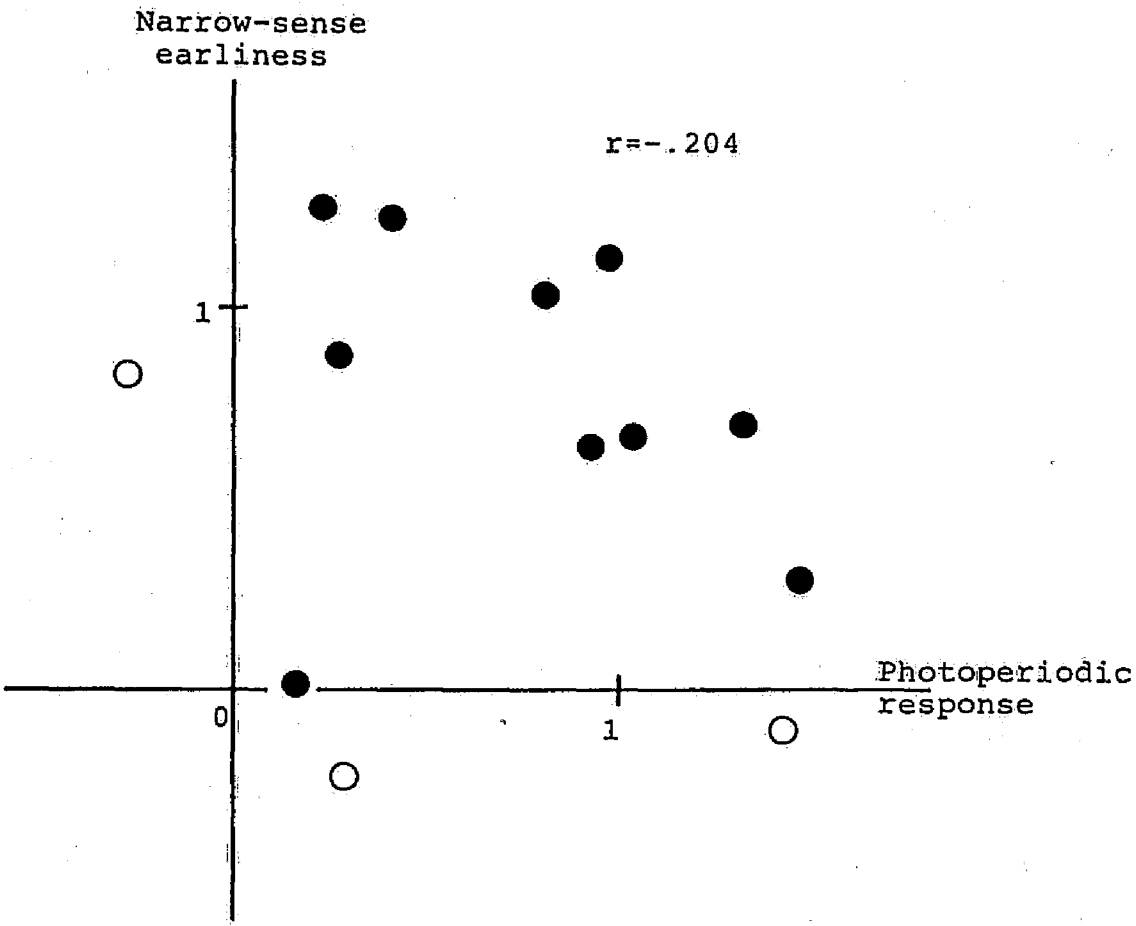

Fig. 13. Scatter diagram of landraces from the northern part of Iran for relative contribution of photoperiodic response and narrow-sense earliness to heading time. Symbols represent heading time of landraces (●;late, ○;early).
See text for the calculation of relative contribution of each trait.

different among landraces, being photoperiodic response or/and narrow-sense earliness. On the other hand, the correlation coefficient was statistically significant in all localities in the Eastern Region ($P<0.01$). In Nepal, late heading landraces exhibited large values both in photoperiodic response and in narrow-sense earliness, while early heading ones exhibited small values in both traits (Fig. 14). This resulted in highly positive correlations between heading time and these two traits. A close relationship was also observed in the Western Region and in Ethiopia (Table 13).

Taking heading time and the combination of the three heading traits into account, there existed three types of landraces in Ethiopia as clearly shown in Fig. 15. The first group was the earliest in heading time due to a weak response to photoperiod, irrespective of a medium chilling requirement. The second group was medium in heading time due to a medium response to photoperiod, though chilling requirement was 0 days. Narrow-sense earliness was not different between these two groups. The third group was the latest in heading time due to a strong response to photoperiod and/or a large narrow-sense earliness, irrespective of chilling requirement.

Discussion

The wheat landraces examined in this chapter showed wide varietal variation in heading time (Fig. 12A), and almost 50% of the variance was explained by differences in origin (Table 10). Since heading time is an adaptatively important character, the

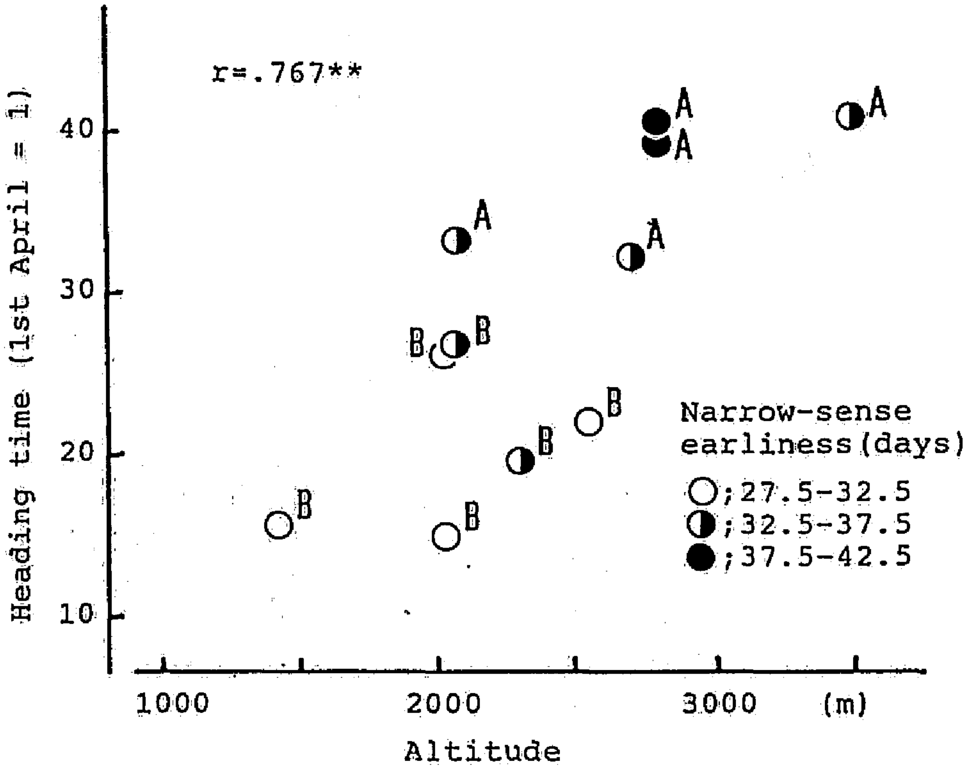

Fig. 14. Heading characters of Nepalese landraces collected at diverse altitudes. Photoperiodic response was represented by alphabetical characters (A;more than 2.1, B;less than 1.6). **; Significant at 1% level.

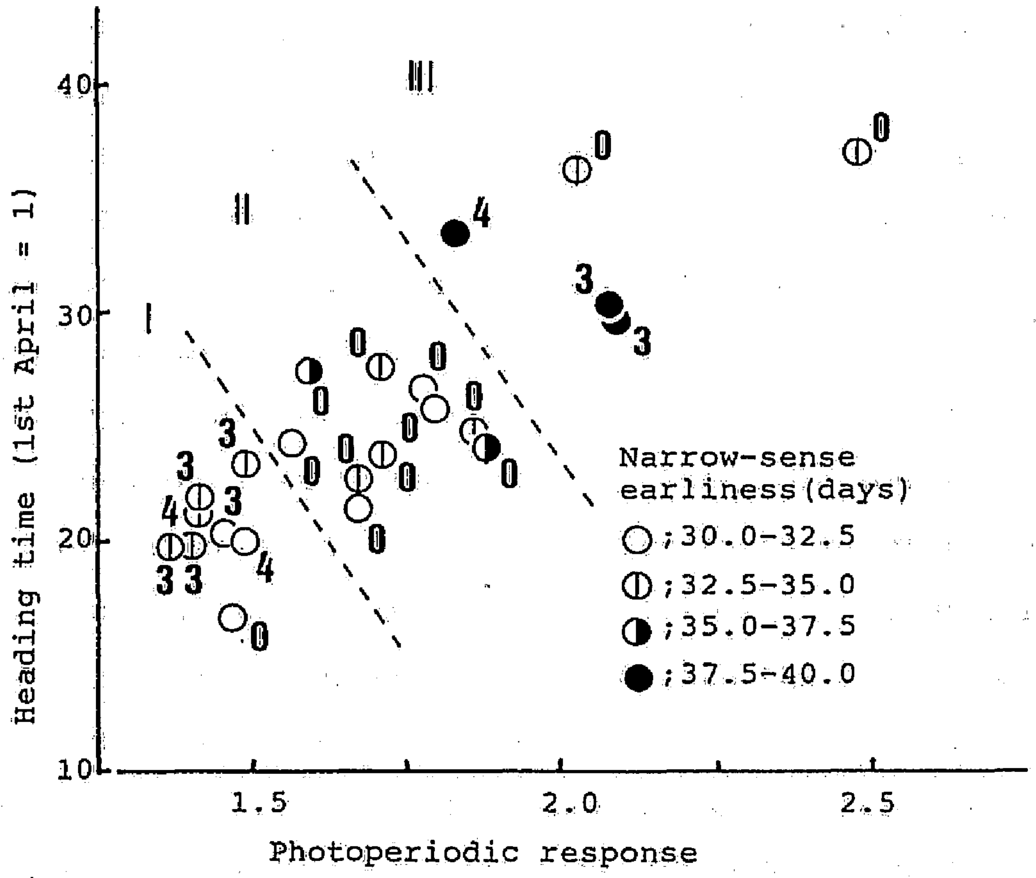

Fig. 15. Relationship between heading time and three heading traits in Ethiopian landraces. Numerical characters represent the tens digit of chilling requirement. Three groups (I, II and III) described in the text were separated by dotted lines.

difference amongst localities can be regarded as the result of adaptation to different growing environments as indicated by MURPHY and WITCOMBE (1981). However, environmental factors limiting wheat adaptation must be different among localities, being temperature, rainfall, photoperiod or others. This fact indicates that the adaptation strategy of a wheat landrace must be separately discussed for each factor or locality.

In the Near East, especially in the areas where annual rainfall is less than 500mm, wheat cultivation is restricted to the period when sufficient water is available (PERRIN de BRICHAMBAUT and WALLEN 1963). Based on this proposal, the month when monthly rainfall is less than 10mm is tentatively shown along with heading time in Table 14. A close relationship between them indicates that the adaptation to an early dry season seems to cause the change towards early heading in the southern part of Iran and Afghanistan as compared with the respective northern part. Such a difference seems to be resulted from the selection forced to avoid the reduction of grain yield caused by water deficit (FISCHER and MAURER 1978; WORLAND et al. 1988). On the other hand, excessive rainfall is also disadvantageous for wheat adaptation. In Nepal, early heading landraces seemed to have been selected to avoid the damage of pre-harvest sprouting caused by monsoonal rain in the early summer. The existence of such a selection pressure was indicated by the fact that all of the Nepalese landraces were of a red kernel type (KATO unpublished) which is generally more resistant to pre-harvest sprouting than white kernel type.

Table 14. Relationship between heading time of landraces and the beginning of dry season in the localities where annual rainfall is less than 500mm

No.	Locality	Heading time	Beginning of dry season month	station[1)]
2	Armenia (USSR)	38.3	8	Yerevan
3	Turkey (East)	40.9	7	Van
4	Iran (North)	40.5	7	Tabriz
6	Iran (South)	32.5	5	Esfahan
7	Afghan (North)	33.3	6	Kabul
8	Afghan (South), Pakistan	28.1	4	Kandahar
12	Egypt, Iraq	23.1	5	Baghdad

1) City where climatic data was recorded

In the areas where sufficient water is available, adaptability of wheat is affected by temperature. A close negative correlation was observed between heading time and average daily temperature in May ($r=-.879$, $P<0.01$), as shown in Fig. 16. It is thus clearly indicated that wheat landraces have been selected for early heading as an adaptation to comparatively warm areas. Such selection avoids the sterility caused by extreme high (KOLDERUP 1979; SAINI and ASPINALL 1982) or low temperature (MARCELLOS and SINGLE 1984; KIM et al. 1985; QIAN et al. 1986), and the reduction in kernel weight under high temperature condition (ASANA and WILLIAMS 1965; SOFIELD et al. 1977). A small deviation from the relationship is observed in the Western Region (Fig. 16), indicating that heading can occur under relatively low temperatures as compared with the other regions. According to KRAMER (1980), such differences may also be explained by adaptation to the hot and dry summers, because it permits early growth to ensure completion of the life cycle before summer.

Using local means shown in Table 12, correlation coefficients were calculated between heading time and the three heading traits. These were all positive and statistically significant ($P<0.01$, data was not shown). However, among the three traits, chilling requirement does not influence the control of heading time of fall-sown wheat varieties, as stated by WORLAND et al. (1988) and also evidenced by the results shown in Table 7, Fig. 9 (CHAPTER III) and Table 13. It is thus indicated that photoperiodic response and narrow-sense earliness become so small as to hasten heading time as an adaptation strategy to water

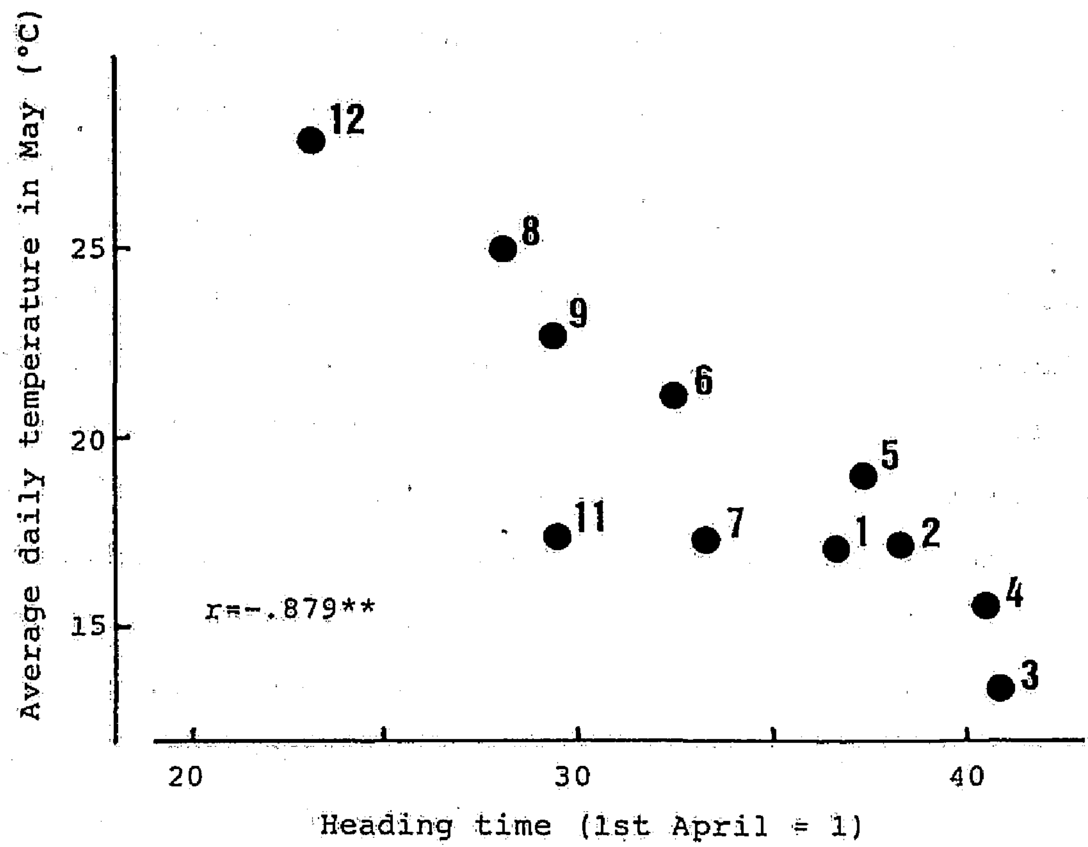

Fig. 16. Relationship between heading time and average daily temperature in May among 11 localities. Numerical characters represent locality No. shown in Table 12.
**; Significant at 1% level.

stress and/or high temperature in the early summer. Correlation coefficients between chilling requirement and monthly average temperature were statistically insignificant from December to March ($r=-.319 \sim r=-.535$), while these were statistically significant in November and in April ($r=-.609$ and $r=-.628$, $P<0.05$). Since average temperature in the latter two months could be regarded as the indicator of the duration of winter coldness, it is suggested that chilling requirement influences adaptation to winter coldness.

A wide variation in environmental conditions should exist within each locality, as it covers a relatively large area in the present study. Because of this diversity, variance component due to varietal difference within localities occupied more than 50% of the whole variation in each character (Table 10). This result indicates that various types of adaptation strategy should come to light by analyzing the relationship between the three heading traits and growing environments in each locality. It was first described for the northern part of Iran, which is a part of the Central Region of wheat evolution. Compared with the other areas in the Near East, the summer is rather cool (Fig. 16) and the beginning of the dry season is late (Table 14). Late heading varieties would thus be able to adapt to such an environment, and actually existed frequently (Fig. 13) because of their long vegetative growth which seemed favorable to obtaining a better grain yield. On the contrary, it seems difficult for early heading varieties to adapt to long winters (Fig. 16), causing the small variation in heading time. The key factor causing late heading proved different among landraces (Fig. 13), as correlation coefficients between heading time and the three heading traits were all statistically insignificant (Table 13). This result clearly indicates that the simple adaptation strategy of retarding heading time was achieved by various combinations of the three heading traits. A wide variation in each trait itself made it possible to keep such diversity. The same phenomenon was also observed also in the other localities in the Central Region (Table 13).

There must be a large diversity in growing environments in Nepal, as landraces were collected from diverse areas whose altitude ranged from 1420m to 3500m. Heading time was delayed with the increase of altitude (Fig. 14), resulting in wide varietal variation. Heading time related closely with both photoperiodic response and narrow-sense earliness (Table 13), though the variation in each trait was not necessarily large. These results indicate that the adaptation strategy dominating in this locality is to control heading time by the exquisite combination of photoperiodic response and narrow-sense earliness. This strategy is suitable for creating wide variation in heading time by combining these traits with less variation. The same strategy was adopted also in the other localities in the Eastern and the Western Regions (Table 13).

Although Ethiopian landraces were also collected from diverse areas whose altitude ranged from 1600m to 2800m, heading time did not correlate with the altitude (r=.324). This result indicates that the limiting factor for wheat cultivation in this locality is not temperature conditions largely affected by altitude.

Landraces were grouped into three, as already mentioned (Fig. 15). The reason for the existence of such a diversity is unknown because heading time in Ethiopia could not be predicted by the results obtained in the present study. Their adaptation strategy was thus speculated by taking the following three points into account. At first, a sufficient vegetative growth is necessary to get a better grain yield, though the length of this period would be restricted by the existence of dry season. Secondly, photoperiodic response causes retardation in heading time because it is a relatively short-day condition. Finally, chilling requirement also causes late heading because temperature is not low enough to vernalize wheat plants. Therefore, to assure a certain level of vegetative growth, the first and the second groups possessed medium degree of chilling requirement and photoperiodic response, respectively (Fig. 15). The third group showed larger values both in photoperiodic response and in narrow-sense earliness, and would be the latest heading also under their native growing environments.

Some landraces showed smaller narrow-sense earliness than Japanese early varieties (Table 9 and Fig. 12D). Some showed larger values both in narrow-sense earliness and in photoperiodic response than North American spring wheat varieties (Table 9 and Fig. 12C,D). Early heading varieties are required in Japan for double cropping with rice and to avoid the damage caused by monsoonal rain. The improved early varieties have already been shown to be insensitive to photoperiod (YOSHIDA et al. 1983), and chilling requirement doesn't influence heading time. The strategy for the breeding of extra-early varieties would thus be to introduce a small narrow-sense earliness from landraces collected from Pakistan, Nepal, Bhutan, Iraq and Egypt. In addition, landraces in the Western Region might be an excellent gene-pool for less growth delay even under low temperature condition. On the other hand, according to WORLAND et al. (1987), long growth period would cause the increase in grain yield under cool summer condition in UK. Although this might be also true in the spring-sowing area at high latitude, natural photoperiod in the early summer is so long that heading time is not necessarily different among wheat genotypes with different photoperiodic response (KNOTT 1986; MARSHALL et al. 1989). Therefore, it should be difficult to control heading time by photoperiodic response in such areas. On the contrary, heading time can be controlled by narrow-sense earliness even under long-day condition, because this trait is regarded as the requirement of cumulative temperature necessary for growing up to heading stage as suggested by MASLE et al. (1989). Therefore, landraces with large narrow-sense earliness can be introduced for the breeding of late heading varieties in these areas.

As heading time has been subjected to strong natural and/or artificial selection, only adapted variants would be selected in each area. Accordingly, environmental heterogeneity within each region should be necessary to keep a wide varietal variation, even in the Vavilovian center of diversity as indicated by MURPHY and WITCOMBE (1981). This seems to be the reason why varietal variation was smaller in the Central Region than in the Eastern Region (Table 11 and Fig. 12A). On the contrary, this situation was not true for the three heading traits and the variation was largest in the Central Region (Table 11). As to photoperiodic response and narrow-sense earliness, such a wide variation seemed to be maintained in the late heading landraces, where insensitivity to photoperiod was accompanied with large narrow-sense earliness and vice versa (Fig. 13). The late initiation of spike primordium in these landraces should be advantageous to avoid cold injury. Therefore, under such a circumstance, even landraces without chilling requirement seems to be able to adapt to winter coldness, resulting in the preservation of wide variation in chilling requirement. From another point of view, a whole range of variation existed in the Central Region in photoperiodic response and chilling requirement, but not in narrow-sense earliness (Fig. 12). Such a discrepancy might be explained by the difference in their genetic systems, which are major genic in the former two traits (PUGSLEY 1972; KEIM et al. 1973) and polygenic in the latter (KATO et al. 1989). In landrace populations, new variant genotype does not appear in major genic trait until spontaneous mutation occurs. But, in polygenic trait, it can easily appear by recombination of minor genes through intra-specific hybridization. This seems to be the reason why genotypes with small narrow-sense earliness, absent in the Central Region, existed in the other regions. It was therefore suggested that wide genetic variation in heading characters could be captured by collecting landraces from the Vavilovian center of diversity, and that environmental heterogeneity should be also taken into account.

Summary

Heading time and the three heading traits, i.e. photoperiodic response, narrow-sense earliness and chilling requirement, were surveyed for 158 wheat landraces. A wide varietal variation was observed in each character. Nearly half of the variation for each character was explained by geographical difference in origin. Based on these data and the growing environments in each locality, adaptation strategy, seen as the adjustment of heading time, was analyzed in terms of the differences in the three heading traits individually and combined. The difference among localities indicated that wheat landraces had been selected for early heading as an adaptation strategy to water stress and/or high temperature in the early summer. This change was caused by a reduction in photoperiodic response and narrow-sense earliness. Chilling requirement was also reduced for adaptation to relatively mild winters. Adaptation strategy deduced from the variation within each locality was also different amongst localities. In the Central Region of wheat evolution, as wide variation existed in photoperiodic response and narrow-sense earliness, late heading trait was achieved by these traits individually or combined. On the contrary, in the Eastern and the Western Regions, a wide variation in heading time was achieved by the exquisite combination of photoperiodic response and narrow-sense earliness. Availability of the landraces as novel genetic resources and a sampling strategy for wheat germplasm were also discussed.

CHAPTER V. GEOGRAPHICAL DISTRIBUTION OF THE GENES FOR CHILLING REQUIREMENT AND ITS IMPLICATION FOR THE ADAPTABILITY OF WHEAT

Introduction

Chilling requirement in wheat is one of the most important characters for adaptation to the cold winters as clearly shown in CHAPTER III, and thus the characters reflecting chilling requirement, namely, growth habit (NAKAI and TSUNEWAKI 1967) and vernalization response (HOOGENDOORN 1985b) show a distinct geographical distribution as well as chilling requirement itself (CHAPTER IV). The difference in chilling requirement in spring wheat varieties is determined by five genes (SEARS 1954; KUSPIRA and UNRAU 1957; MORRISON 1960; TSUNEWAKI and JENKINS 1961; LAW 1966; TSUNEWAKI 1966; HALLORAN and BOYDELL 1967; PUGSLEY 1971,1972). Among these _Vrn1_ is the most effective and gives complete insensitivity to vernalization as shown in CHAPTER II. The three other genes, _Vrn2_, _Vrn3_ and _Vrn4_ give partial insensitivity, with _Vrn2_ being weaker than the other two genes (GOTOH 1976). Therefore, the non-random geographical distribution of chilling requirement (Table 12 and Fig. 12) can be explained by the adaptation of particular vernalization genes to the specific environment in each region. STELMAKH (1986) studied the relationship between geographical origin and the frequency of three genes, _Vrn1_, _Vrn2_ and _Vrn3_, using 574 spring wheat varieties from various countries, but failed to show any clear-cut pattern, probably because the varieties studied were artificially selected for earliness. This work may therefore be more suitable in tracing the history of systematic breeding, rather than in the analysis of adaptability of Vrn genes.

In this chapter, therefore, the geographical distribution of Vrn genes was studied by using wheat landraces, and the reasons for their different distribution were discussed by taking into account the growing environments in each region and the heading traits of each variety.

Materials and Methods

Eighty-three wheat landraces collected from the various countries shown in Table 15 were examined. Seed of 76 varieties were supplied by the Plant Germ-plasm Institute, Kyoto University, Japan, and 8 from the National Agricultural Research Center (NARC), Japan.

Genetic analysis: To identify the Vrn genotype, each variety was crossed with a series of Pugsley's near-isogenic lines of 'Triple Dirk', each of which has one gene pair of vernalization genes, namely, Vrn1, Vrn2, Vrn3 or Vrn4. The seed of these lines were supplied from the Tohoku National Agricultural Experiment Station, Japan. F_2 populations and parental lines were grown in a glasshouse under a regime of 24 hour day-length. They were sown in soil-filled containers at a spacing of 2cm (between hills) X 3.5cm (between rows). Six plants and 180 plants were allotted to each parental line and each F_2 population, respectively. The number of days from sowing to flag leaf unfolding or the number of vegetative rossette segregants was determined.

Heading characters: Heading characters were measured for 76 wheat landraces from Plant Germ-plasm Institute in Chapter II. These data were used for the analysis of the relationship between the Vrn genotype, heading characters and the growing environments in each region. However, 8 varieties from NARC were excluded from such an analysis, as their heading characters have not been studied.

Results and Discussion

The frequency distribution of the number of days from sowing to flag leaf unfolding observed in the F_2 populations from crosses of 'IL 47' from Turkey and the four near-isogenic testers was shown in Fig. 17. Winter plant type, which was homozygous recessive at all four loci, was not observed in the crosses with 'Triple Dirk(D)' and 'Triple Dirk(F)', but occurred with a frequency of 1/64 in the crosses with 'Triple Dirk(B)' and 'Triple Dirk(E)'. Therefore, it was concluded that 'IL 47' had both Vrn1 and Vrn4.

In the same manner the genotype of each variety was identified (Table 15). Although 15 genotype combinations were possible with four segregating genes, only 13 genotypes were actually identified. Two genotypes, one having both Vrn2 and Vrn4 and the other having dominant genes at four loci were not detected. Besides these, 5 varieties from the Central and Eastern Regions (Afghanistan, Pakistan and China) were thought to carry

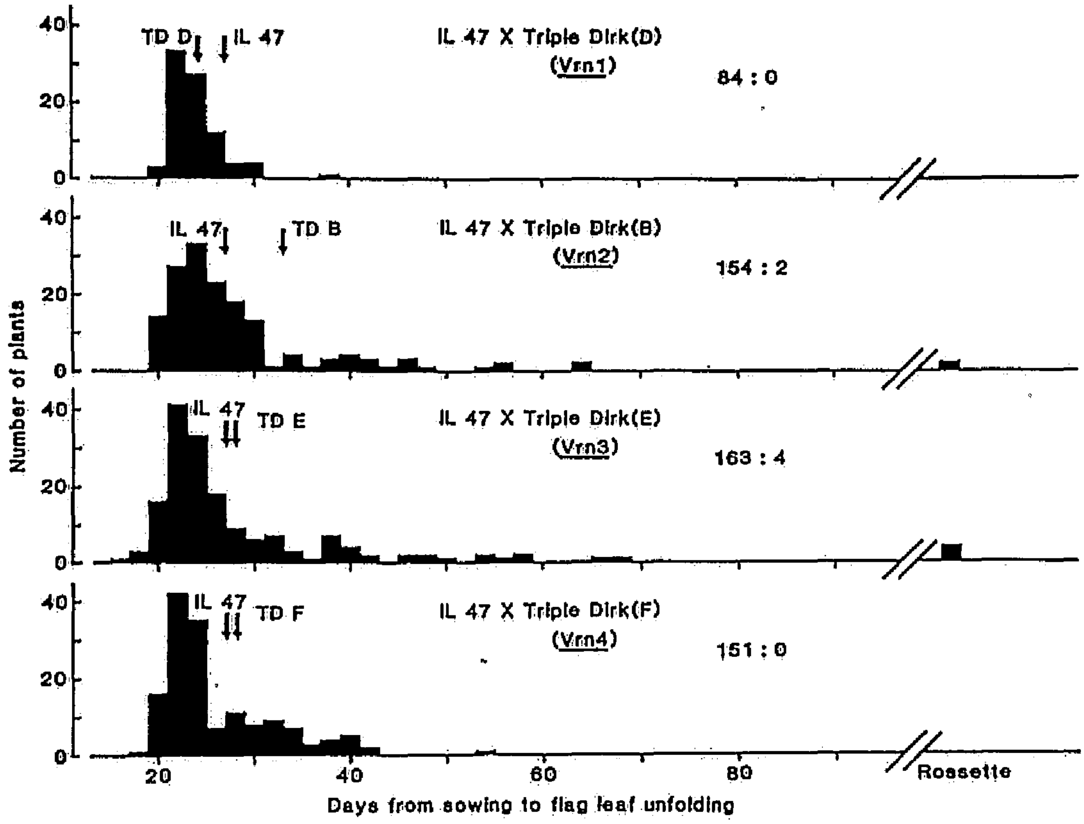

Fig. 17. Frequency distribution of the days from sowing to flag leaf unfolding in the F_2 populations derived from the crosses between 'IL 47' and four near-isogenic lines of 'Triple Dirk'.
TD B,D,E and F refer to each near-isogenic line of 'Triple Dirk'.
Arrows indicate the days to flag leaf unfolding of parental lines.

Table 15. Genotypes for chilling requirement isolated in wheat landraces and their frequency in each region

Region[1)]	No. of landraces	Vrn genotype[2)]													
		1	1,2	1,3	1,4	1,2,3	1,2,4	1,3,4	2	3	4	2,3	3,4	2,3,4	U
Center	19	2	1	3	0	1	1	0	1	7	1	0	0	0	2
West	9	1	1	0	1	0	0	0	3	2	0	1	0	0	0
South(I)	8	1	1	1	2	1	0	1	0	0	0	0	0	1	0
South(II)	20	0	11	0	0	0	0	1	2	4	1	1	0	0	0
East	27	0	1	0	3	0	0	0	3	12	3	0	2	0	3
Total	83	4	15	4	6	2	1	2	9	25	5	2	2	1	5

1) Each region consisted of the following countries.
Center ;Iran, Afghanistan(northern area), Armenia(USSR), Turkey(mountainous area)
West ;Turkey(coastal area), Greece, Italy
South(I) ;Iraq, Egypt, South(II);Ethiopia
East ;Afghanistan(southern area), Pakistan, Nepal, Bhutan, China, Japan
2) Each numeric character refers to the Vrn gene(s) present. U = unknown

vernalization genes other than the four genes tested for. It was not possible to determine if the new genes include Vrn5 (LAW, 1966). Therefore, the geographical distribution of these genes was not discussed here. The frequency of each genotype was clearly different among the regions, especially between the Southern(II) and the Eastern Regions. While more than half of the varieties from the Southern(II) Region had both Vrn1 and Vrn2, about half of the varieties from the Eastern Region had only Vrn3.

The total number of genes presented in each region was very variable (Table 16). Vrn1, Vrn2 and Vrn3 were frequent and Vrn4 was less common. The relative frequency of each gene against the total number of varieties also differed amongst the regions varying from 15% to 88% for Vrn1, from 15% to 70 % for Vrn2, from 30% to 54% for Vrn3 and from 10% to 50% for Vrn4. Compared to the frequency in the Central Region, increases in the Southern(I and II) Regions and decreases in the Western and the Eastern Regions were observed for Vrn1. Increases in Vrn2 frequency in the Western and the Southern(I and II) Regions and increases in Vrn4 frequency in the Southern(I) and the Eastern Regions were also observed. Vrn3 was fairly evenly distributed across the various regions.

According to STELMAKH (1986), the frequency of Vrn1 and Vrn2 was more than 70% and 50%, respectively, in all regions, and the frequency of Vrn3 was less than 30% in all regions. The frequency of each gene except Vrn3 showed no clear difference among the regions. Although the result obtained in this chapter

Table 16. Total number of Vrn genes isolated and their relative frequency in each region

Region	No. of landraces	No. of genes[1]						Chi-square[2]
		Vrn1	Vrn2	Vrn3	Vrn4	unknown	Total	
Center	19	8(42)	4(21)	11(58)	2(11)	2	27	2.78
West	9	3(33)	5(56)	3(33)	1(11)	0	12	1.82
South(I)	8	7(88)	3(38)	4(50)	4(50)	0	18	2.52
South(II)	20	12(60)	14(70)	6(30)	2(10)	0	34	7.83*
East	27	4(15)	4(15)	14(54)	8(31)	3	33	9.38**
Total	83	34(41)	30(36)	38(46)	17(20)	5	124	

1) Numbers in parenthesis show the relative frequency(%) of each Vrn gene against the number of landraces in each region.
2) Fit to the overall frequency of Vrn1, Vrn2, Vrn3 and Vrn4
*,**; Significant at 5% and 2.5% level, respectively.

Table 17. Difference in three heading characters[1] of wheat landraces among five regions

Region	No. of landraces	Heading time	Photoperiodic response	Narrow-sense earliness(days)
Center	19	31.4	2.00	35.4
West	9	25.7	1.66	34.4
South(I)	8	22.6	1.66	33.1
South(II)	20	26.8	1.74	34.0
East	19	24.2	1.65	33.2

1) Values are shown in varietal mean in each region.

differed from these, the discrepancy was considered to be ascribable to STELMAKH's use of modern varieties, in which the worldwide distribution of Vrn1 might result from the breeding of early varieties.

The results for heading characters were shown in Table 17, and the relationship between Vrn genotype and heading characters was shown in Fig. 18. Apart from Afghan materials, varieties from the Central Region were late-heading, owing to their strong response to photoperiod and large narrow-sense earliness (Table 17). However, heading time was independent of Vrn genotype (Fig. 18A). In addition, almost all varieties, including those carrying Vrn1, showed rossette habit in the field during the winter. These observations suggested that varieties adapted to relatively mild winter by means of strong response to photoperiod, large narrow-sense earliness and rossette habit, but not due to the presence of particular Vrn genes. On the other hand, Vrn1 was less frequent in the Western and the Eastern Regions and in Afghanistan. In the Western Region, only early varieties with weak response to photoperiod and small narrow-sense earliness adapted well to avoid the hot and dry summer (Table 17 and Fig. 18B). However, early varieties having Vrn1 might be liable to injury from occasional low temperature in the early spring if these occurred following a warm winter. This resulted in a decrease in the frequency of Vrn1 (Table 16). In Afghanistan where winter coldness was severe, only carriers of Vrn genes giving a chilling requirement were adapted (Figs. 18A and 19). Similarly, as in the Western Region, this tendency arose in the Eastern Region where early varieties adapted to

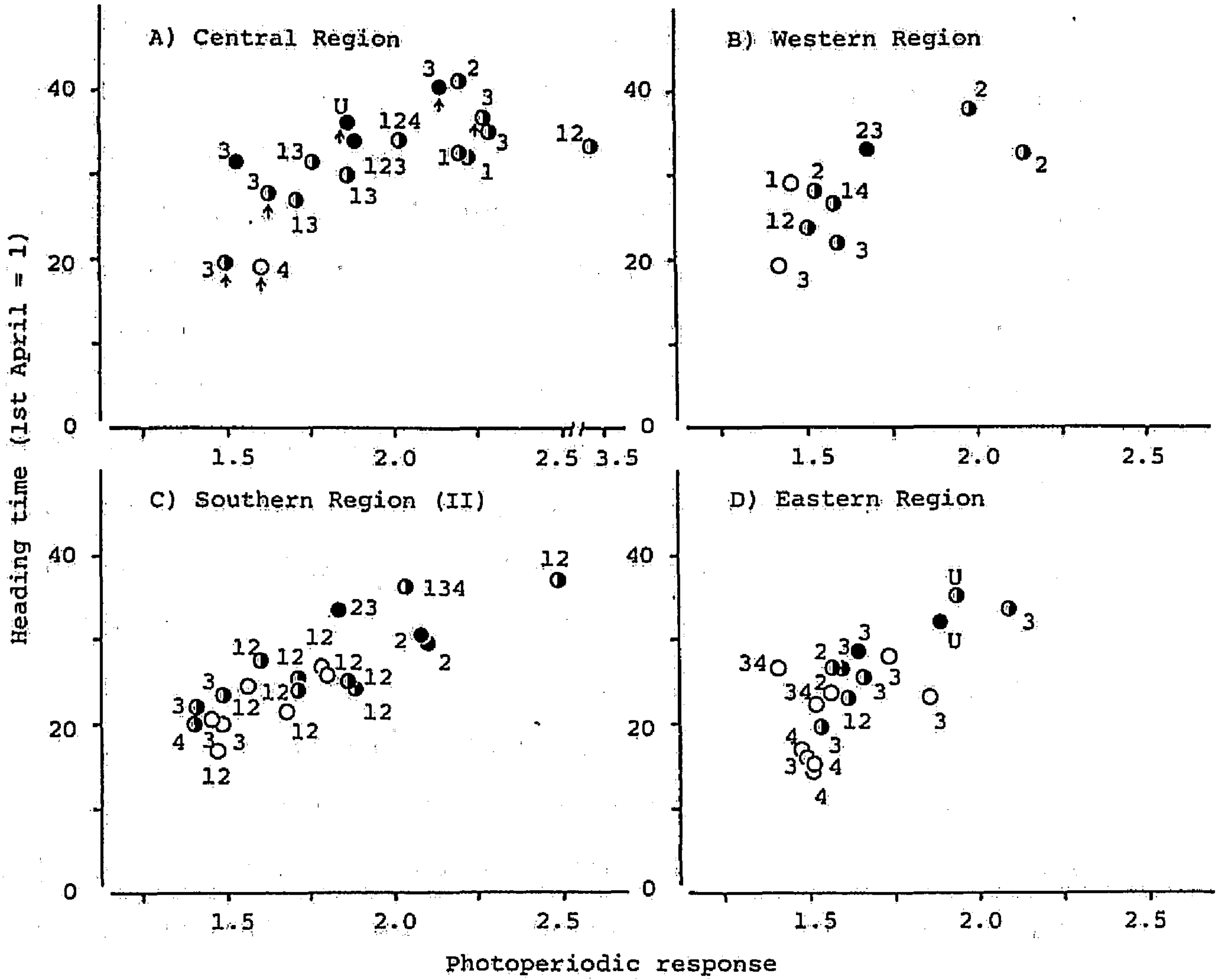

Fig. 18. Relationship between Vrn genotype and heading characters in each region.
Numeric characters represent the identity of the Vrn genes in each landraces.
Landraces from Afghanistan are showed by arrows.

avoid heavy monsoonal rain in the early summer. These changes in the frequency of Vrn1 with the spread of wheat were illustrated in Fig. 19. In the Southern(I and II) Regions, the temperature is not low enough to satisfy chilling requirement, resulting in an increase in the frequency of Vrn1 (Table 16).

As mentioned above, a change in the frequency of Vrn1 with the spread of wheat could be explained as the result of adaptation to respective growing environments. The other three Vrn genes can be considered in two groups. One group of varieties combines an additional gene with Vrn1, and thus the extra gene is not expressed. The second group of varieties lack of Vrn1, and thus express the additional gene. The frequency of these genes in the two categories was summarized in Table 18. Among the varieties in the latter category where the gene was important from the stand point of adaptation, Vrn3 was the most frequent and widespread. Compared to the frequency in the Central Region, Vrn2 was more common in the Western and the Southern(I and II) Regions, and Vrn4 was more common in the Eastern region. The three genes, however, all give a slight chilling requirement, which is essential for adaptation to fall-sowing in these regions. Although varieties having only Vrn4 were consistently earlier in each region, heading time of varieties with only Vrn2 or Vrn3 differed between the regions (Fig. 18). Varieties with Vrn2 headed later in the Southern(II) and the Western Regions than those having Vrn3, while they are not necessarily later in the Eastern Region. This suggested that the distribution of Vrn4 could be the result of adaptation of early heading varieties, and

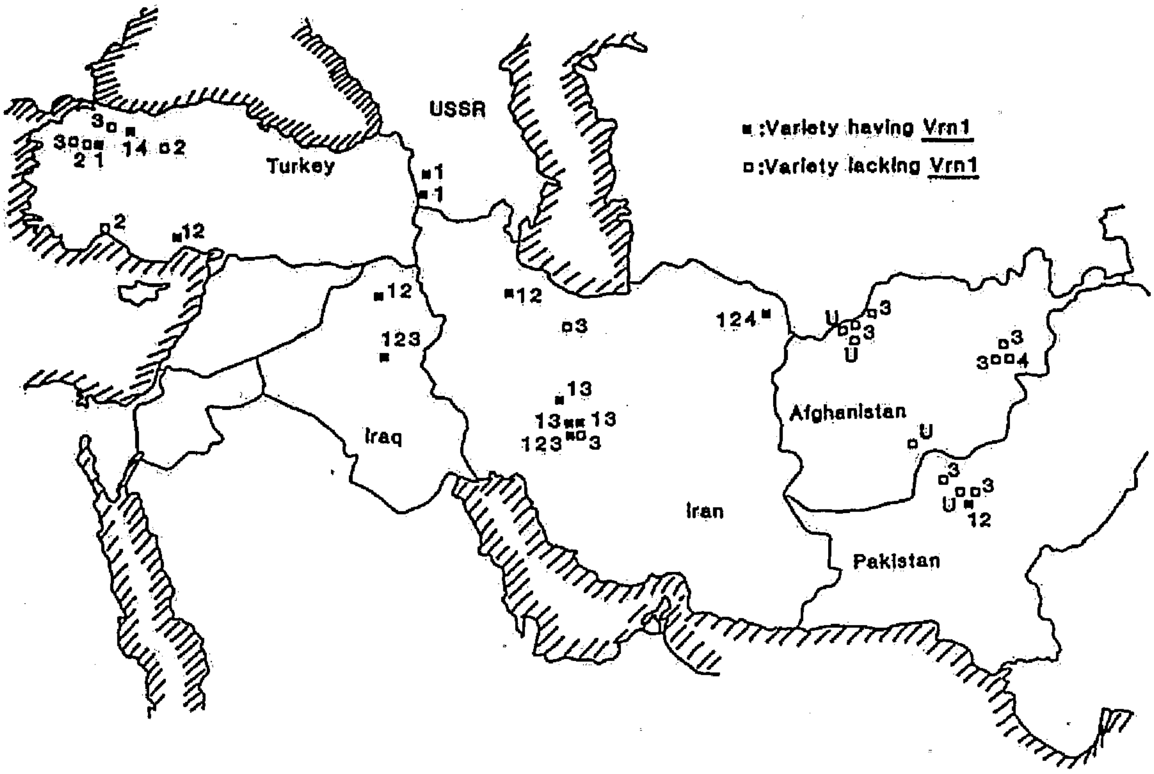

Fig. 19. Relationship between Vrn genotype and collection site of each landrace in the Central Region and the surrounding areas.
Numeric characters represent the identity of the Vrn genes in each landraces.

Table 18. Number of landraces carrying each Vrn gene with or without Vrn1 in each region

Region	Landraces lacking Vrn1				Landraces having Vrn1			
	Vrn2	Vrn3	Vrn4	unknown	Vrn2	Vrn3	Vrn4	null
Center	1	7	1	2	3	4	1	2
West	4	3	0	0	1	0	1	1
South (I)	1	1	1	0	2	3	3	1
South (II)	3	5	1	0	11	1	1	0
East	3	14	5	3	1	0	3	0
Total	12	30	8	5	18	8	9	4

that the distribution of Vrn2 might not be the result of its adaptability, but rather due to the selection for other linked genes.

The frequency of the genes in varieties having Vrn1 showed that Vrn2 was very frequent in the Southern(II) Region (Table 18). This distribution is obviously independent of adaptation, and may be related to the distribution of Vrn2 in the Western and the Southern (II) Regions mentioned above. Thus a more detailed study, including linkage relationship with Vrn2 is needed. In this connection, the three genes were fairly frequent in the Southern (I) Region and were quite different from the frequencies found in the Southern (II) Region. This discrepancy may reflect the different origins of introduced wheat (ZEVEN 1980).

The Japanese variety 'Akabozu', examined in this study, carried only Vrn3, as do indigenous Japanese spring wheat varieties (GOTOH 1979a). As mentioned above, Vrn1 disappeared on moving east. In the Eastern Region, heading time varied between Vrn genotypes. Most of the varieties having only Vrn3 were the last to head (Fig. 18). Four Chinese varieties from fall-sowing areas, three of which carried only Vrn3, were also late heading (KATO and HAYASHI unpublished). These results suggested that late spring varieties were selected with the spread of wheat to China through mountainous regions, resulting in the selection for Vrn3. The distribution of Vrn3 in Japan, therefore, may reflect the frequency of Vrn genes in China. This would imply that Vrn2 and Vrn4 may be effective for practical breeding in Japan and that Vrn4 may be suitable for the breeding of early varieties. However, as little is known about this gene, the function, chromosomal location and linkage relationships with other genes should be studied.

Summary

Geographical differences in the distribution of genes responsible for chilling requirement were detected among 83 wheat landraces collected from various countries. The frequency of varieties having *Vrn1*, which was the most effective and was epistatic to other genes, was clearly different between the regions. In varieties lacking *Vrn1*, *Vrn3* and *Vrn4* were frequent in Asia, while *Vrn2* was frequent in Ethiopia and the Mediterranean region. Taking the growing environments in each region and heading characters of each variety into account, the distribution of *Vrn1* was well explained as the result of the adaptation of each variety to respective growing environment. On the other hand, the distribution of *Vrn2*, *Vrn3* and *Vrn4* could not be explained with respect to their adaptability, as the functions of these genes are similar.

CHAPTER VI. CONCLUSIONS

As a basic research to know the breeding strategy of heading time in wheat, the present study was carried out to show how each heading trait influences the adaptability. As the first step of this study, the evaluation method was established for the three heading traits, namely, chilling requirement, narrow-sense earliness and photoperiodic response. Then, using wheat landraces of diverse geographical origins, adaptation strategy through the adjustment of heading time was discussed by analyzing the relationship between heading time in the field, the three heading traits and growing environments at their geographical origins. Finally, genetic aspects of such an adaptation strategy was discussed for chilling requirement. The conclusions made from the present study are summarized as follows.

1. Evaluation method of the three heading traits

To establish the evaluation method of chilling requirement, plant-development model was designed as to the change of unfolding time of the 1st leaf and flag leaf in response to chilling treatment duration (Figs. 1 and 2). Through a series of experiments, Dt1 (See Table 1) decreased in proportion to the treatment duration (Table 3 and Fig. 4). Furthermore, Dof (See Table 1) reached the respective constant values with the increase of the treatment duration (Table 4 and Fig. 5). As these results clearly showed the adequacy of the above-mentioned model, it was concluded that by using Dof as an index chilling requirement could be measured as the minimum duration of chilling treatment necessary for full vernalization. Narrow-sense earliness could be also measured by the Dof of fully vernalized plants.

To establish the evaluation method of photoperiodic response, the precision of the measurements of photoperiodic response was compared between two measures calculated as the difference in and as the ratio of the growth periods of fully vernalized plants between long-day and short-day conditions. Correlation coefficient between narrow-sense earliness and the two measures of photoperiodic response was calculated for wheat landraces which showed a wide varietal variation in each heading trait, and it was found to be higher in the difference than in the ratio (Table 7). This result indicated that photoperiodic response measured as the difference partly included the effect of narrow-sense earliness. Therefore, photoperiodic response should be measured as the ratio of the growth period under short-day condition to the one under long-day condition.

2. Relationship between heading time and the three heading traits

The relationship between heading time and the three heading traits was analyzed for wheat landraces. Although simple correlation coefficients were all positive and statistically significant, partial correlation coefficient was statistically insignificant between heading time and chilling requirement (Table 7). In addition, almost the whole variation in heading time was covered by the varieties whose chilling requirement was estimated at 0 days (Fig. 9). These facts clearly indicated that chilling requirement was not an important trait in the control of heading time, but necessary for the adaptation to winter coldness. On the other hand, partial correlation coefficients of photoperiodic response and narrow-sense earliness on heading time showed similar values with each other and were both statistically significant (Table 7). It was thus concluded that narrow-sense earliness was as important in the control of heading time as photoperiodic response, though this trait was formerly considered as a minor factor. However, the mechanisms to control heading time seemed to be different between these traits. Photoperiodic response controls heading time so as to occur on the same calendar date every year, while narrow-sense earliness controls it through the requirement of cumulative temperature necessary for growing up to heading stage.

3. Adaptation strategy through the adjustment of heading time

Heading time and the three heading traits were compared between wheat landraces of different geographical origins. It was clearly shown that nearly half of the whole varietal variations was ascribable to the differences in the regions or localities (Table 10). The following adaptation strategy was deduced from the analysis of geographical difference in the heading traits and growing environments. The major environmental factors limiting the adaptability of wheat varieties proved to be high temperature and drought in the early summer and coldness in the winter (Table 14 and Fig. 16). The comparisons between regions showed that wheat landraces seemed to be selected for early heading, which was achieved by the reduction in both photoperiodic response and narrow-sense earliness, as an adaptation strategy to the two environmental stresses, i.e. heat and drought (Table 11). Increase in chilling requirement resulted from the adaptation to relatively severe winters. On the contrary, the adaptation strategy adopted within localities was not necessarily uniform but varied for different regions, depending on the variations in each heading trait and in growing environments (Table 13 and Figs. 13,14 and 15).

4. Adaptation strategy and genes responsible for chilling requirement

Relative frequency of each Vrn gene carried by wheat landraces was different amongst the regions of their geographical origin (Table 16). The heading traits of landraces and growing environments at their geographical origins were analyzed to find out the reason for such a geographical difference. In the Central Region, Vrn genotype of landraces seemed to be independent of their adaptability, because they adapted to relatively mild winters by means of late heading which was caused by the two heading traits other than chilling requirement (Table 17 and Fig. 18A). In the other regions where heading time of landraces was relatively early, Vrn genes played an important role in the adaptation to winter coldness. This conclusion was reached on the account of the fact that the adaptation to warmer and colder winters resulted respectively in the increase and decrease of the frequency of Vrn1 compared with their frequency in the Central Region (Table 16). However, geographical difference in the frequency of the three other genes could not be explained in terms of their adaptability. Therefore, further study is necessary to explain the geographical differences between the three genes.

Precise evaluation of the three heading traits and the results obtained in this study showed that each of the three heading traits influenced the adaptability of wheat varieties in a different way. It was thus inferred that the adaptability should be improved efficiently by combining the three traits properly. However, to improve the efficiency of such a breeding strategy, further study on the interactions between the three heading traits is necessary by using well decorated genetic materials.

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